Revealing mnemonic representations of the body in the brain.

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List of artwork

During my PhD I have created artistic impressions (artwork images) to convey complex concepts to non-scientific audiences. This process resulted in a synergy between science and art that helped me to develop new ideas. In my photographs I used “brushes of light” against the models’ body surface during long exposure and other techniques that vanish the bodies into light. I have included a selection of these images at the end of the chapters.

Visual realm – Merged landscapes: Vision I – VI

Bodily realm – The Method

Bodily realm – Escher’s allegory

Portraits of thin air: AL, Duo, IR

Bodily realm – Tactile or motor?

Bodily realm – Multidimensional bodies

Bodily realm – Body deconstruction or ‘tortilla de patatas’

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Declaration

I grant powers of discretion to the University Librarian to copy the whole, as well as sections of this thesis without further reference to me. This covers only single copies for study and research purposes. The contents of this thesis are subject to standard conditions of acknowledgement. Last, the content of this thesis is my own work except where stipulated.

Abstract

Current accounts in the memory field suggest that perceptual mechanisms underpin both perception and memory processes. The overlap between perceptual and mnemonic mechanisms has been mainly shown when processing arbitrary stimuli (e.g., shapes and colours). Nevertheless, it still unclear how more socially meaningful stimuli such as others' bodies are perceived and later maintained in memory.

This thesis investigates the encoding and memory maintenance of visually perceived body-related information. *Chapter 1* reviews current accounts in the overall memory field. Secondly, it reviews evidence for the presence of a memory system to encode and maintain body-related information in working memory. *Chapter 2* describes the EEG technique and proposes a novel method to isolate brain activity arising in sensorimotor cortex from concomitant visual activity that is elicited at the sight of visually perceived body stimuli. *Chapter 2.5* outlines how the stimuli for the experiments of this thesis were created. *Chapter 3* reports the first study looking into the transformation of visual bodily percepts into mnemonic body representations. This was done by adapting well-known working memory paradigms and the EEG method outlined in *Chapter 2*. The results showed that holding in memory body-related stimuli involves visual acquisition but quick recoding of the visual input onto somatosensory cortices. *Chapter 4* includes another new EEG study that allowed exploration of more anterior brain areas (i.e., motor regions) during memory maintenance of body images in memory. To this end, visual-evoked potentials were combined with motor-cortical potentials. *Chapter 5* followed up the two previous EEG studies with three different behavioural versions centred on interfering with the on going processing of body stimuli. Specifically, different forms of sensorimotor suppression were applied during encoding and maintenance of body-related information in memory. Altogether, the

methodology and experiments of this PhD work suggest that compared to mnemonic processing of non-body-related images, holding body-related stimuli in memory (beyond the perceptual stage) recruits brain areas such as somatosensory and motor cortices. Finally, *Chapter 6* reflects on the results of these studies, offering an overview of this PhD work, as well as on the limitations, technicalities, and potential future studies.

Abbreviations

AON: Action observation network

CDA: Contralateral delay activity

CE: Central executive

CNV: Contingent negative variation

dPMC: dorsal primary motor cortex

EBA: Extrastriate body area

EEG: Electroencephalography

ERP: Event-related potential

FBA: Fusiform body area

FFA: Fusiform face area

fMRI: Functional magnetic resonance imaging

IPS: Instraparietal sulcus

LTM: Long-term memory

MCP: Motor-cortical potential

MVPA: Multivoxel pattern analysis

N2pc: Negative posterior contralaterality

PFC: Prefrontal cortex

RP: Readiness potential

RT: Reaction time

SEPs: Somatosensory-evoked potentials

S1: primary somatosensory cortex

SMA: supplementary motor area

STM: Short-term memory

tCDA: tactile contralateral delay activity

vCDA: visual contralateral delay activity

vdCDA: visually-driven contralateral delay activity

vdN2cc: Visually-driven negativity central

VEP: Visual-evoked potential

vPMC: ventral primary motor cortex

VSSP: visuo-spatial sketchpad

WM: Working memory

1 Chapter 1: Introduction

Human cognition is ultimately grounded in three processes: encoding, maintenance, and recall of information. In the encoding stage, external events are perceived through our senses and transformed into mental representations. For instance, seeing a human body does not simply involve the perception of colour and contours, but its transformation in the brain into an internal body representation. By doing this, we move from mere visual information to functional and meaningful cognition that allows us to understand, imitate, and learn from others' bodies. However, while there is a reasonably good understanding of the neurocognitive mechanisms behind the processing of arbitrary visual stimuli such as colours and shapes, less is known about the mechanisms underpinning encoding and maintenance of visually perceived body-related information. Specifically, it is unclear how such visual-to-body mnemonic representations are accomplished in the brain.

In order to understand what memory for body-related information is and why it needs to be studied, it is essential to portray the subject within the overall memory framework. In this chapter I first outline general models and behavioural studies in memory processing, particularly in the working memory (WM) domain. Secondly, I revise more recent models based on brain imaging and electrophysiological studies. Third, I introduce the image of the body as a unique type of visual stimulus, as well as revising behavioural studies on sensorimotor memory —related to memory processing of visually perceived bodies and actions. Lastly, I consider the potential neural candidates of the latter processing and I formulate a novel theoretical model, which will be explored in the later experimental chapters.

1.1. Introducing working memory

Let's start from scratch in reasoning about the fundamental purpose of memory, and therefore, in which ways it operates. Our senses collect information depicting potential interactions with the surroundings. This perception, in the service of action, does not emerge in a cognitive vacuum but in a functional frame that requires updating and learning information. This postulate entails, at least, three statements that will guide the rest of this piece of work: i) perception is malleable, ii) actions are purposeful and feedback upon perception, and iii) the interaction between both processes requires a mechanism affecting prospective behaviour. Here, perceiving and acting upon the environment (e.g., approaching a neuroscience book or trying a new dish) are meaningless if they do not affect the way one will behave later in time, and this requires information to be stored.

Memory comprises the process in which a perceived event is codified in terms of demands and material (encoding), consolidated in a way that the transient percept can be later accessed (storage), and recalled from storage to be used (retrieval). While these processes are true for any given type of memory-representation, memory processing has been split in several types, components, and subsequent frameworks. This division is not arbitrary but functional, and it can be traced to the work of William James, who already established a distinction between primary and secondary memory (James, 1890). The former refers to the initial storage, in which information is currently available, whereas the latter refers to those memories that require active and conscious access (i.e., actively inspecting past information); a valid distinction that would be later examined with modern techniques (Cowan, 1995; Soto et al., 2011; Soto and Silvanto, 2014).

One of the most important contributions to current models of memory processing, especially for working memory (WM) models, comes from the multi-component

memory model of Atkison and Shiffrin (1968). This model portrays several mnemonic stages in which information is processed via different memory stores. Initially, sensory information is merely acquired. Secondly, it is encoded through strategies such as rehearsal and chunking. The latter stage fosters the information from a fragile state into a more consolidated form that can be accessed from long-term memory. The model of Atkison and Shiffrin could explain some aspects of memory performance such as primacy and recency effects (Glanzer, 1972), as well as data from specific cases of amnesic patients (Shallice and Warrington, 1970; Scoville and Milner, 1957). However, it possessed several important limitations: first, it assumed that holding information in short-term memory (STM) guarantees its transference to long-term memory. Secondly, it assumed that deficits in the short-term store would lead to impaired maintenance of on-going information. Thirdly, the short-term store was a form of mandatory period/step to reach a long lasting memory association. All three assumptions have proven to be wrong (see Baddeley and Levy 1971; Craik and Lockhart, 1972; Craik 2002).

The 'all or nothing' trait regarding the flow of information in the multicomponent-model, its oversimplified linear course, and the incoming view of short-term storage as a more dynamic system, led researchers to shift their theoretical approach and experimental paradigms examining memory storage. While the multicomponent-model declined, the understanding of STM as a workspace to hold in memory task-relevant information (namely, working memory; WM) steadily increased.

1.1.1. The multicomponent model of working memory

The current term 'working memory' (WM) developed from the preceding STM concept, (in many cases both are still indistinguishably used). However, while STM refers to the transient storage of information, WM involves temporary maintenance of information and its manipulation (Baddeley, 2012). STM can also be understood in

the context of experimental designs or in the context of a theoretical system to store information. In the first case, STM would refer to those experimental tasks in which information to-be-remembered is stored over a short delay. Despite this, results from STM paradigms are likely to reflect both STM and LTM associations (Waugh and Norman, 1965; Atkinson and Shiffrin, 1968; Baddeley 2012).

The seminal paper of Baddeley and Hitch (1974) broke apart the multicomponent-model of Atkison and Shiffrin (1968). The authors proposed three inter-related subsystems instead of a unitary one, in which information is not only stored but also manipulated (i.e., storing while working in the information). The three subsystems were delineated when examining the capacity limits in memory processing, that is, the quantity of information that can be stored in memory (see Miller, 1956; Baddeley and Hitch, 1974). Previous studies showed that concurrent tasks to the memory task disrupt memory performance by exhaustion of common computational resources. Examples of concurrent tasks, also known as secondary or suppression tasks, comprise a wide range of experimental manipulations that aim to target specific functions and memory systems. Overall, these include perceiving, reasoning, and handling different types of information during the encoding and consolidation in memory of the stimuli to-be-remembered (e.g., words, numbers, spatial locations, digits, body movements, and so on).

Despite Baddeley and Hitch showing decreases of memory performance by the use of concurrent tasks aiming to overload STM, in some cases participants' performance did not break down. Instead, they observed a monotonic decrease in memory performance, which did not interact with memory load. Importantly, constant decreases in memory performance (when performing a concomitant task) are usually driven by general effects of cognitive load such as binding of information, whereas a break down in performance typically indicates an overloading of a particular memory

system. In both cases general processes such as binding and attentional mechanisms are present. However, in the second case, once the memory limit is reached, a prompt decay in memory performance can be observed (Cocchini et al., 2002; Logie, Zucco, Baddeley, 1990; Repovš and Baddeley, 2006). Overall, by combining different types of concurrent-secondary tasks with memory tasks, Baddeley and colleagues 'manufactured neuropsychological patients', allowing them to reveal the presence of several non-overlapping memory systems.

The initial multi-component model of WM (Baddeley and Hitch, 1974) (Figure 1-1) included three systems: a multidimensional code integrating information (central executive) and two slave systems storing semantic and visuo-spatial information. The term slave refers to a model of communication protocol, a concept borrowed from computer sciences and engineering, denoting hierarchy and direction of control from master to slaves systems. The three systems were defined as follows: the central executive (CE) exerts the role of a central controller regarding attentional control of action. Secondly, the phonological loop is a modular system that stores and holds verbal information by vocal and subvocal rehearsal. Different manipulations have shown that memory for verbal information decreases with concomitant verbal processing, overwriting and displacing its content. For instance, phonological similarity of the stimuli to-be-remembered decreases memory performance, affecting the correct recall and order of the information (Watkins, Watkins, and Crowder, 1974; Lewandowsky and Farrell, 2008). Holding in memory longer words, which take longer to vocalize and process, increases the chance of decay and leads to worse retrieval (Baddeley et al., 1975; Hurlstone et al., 2014). Also, articulatory suppression (i.e., concurrent verbal task) seems to depend on internal speech or subvocalization. Obstructing this subvocalization nullifies the aforementioned word length and phonological effects (Baddeley et al., 1975; Baddeley and Larsen, 2007).

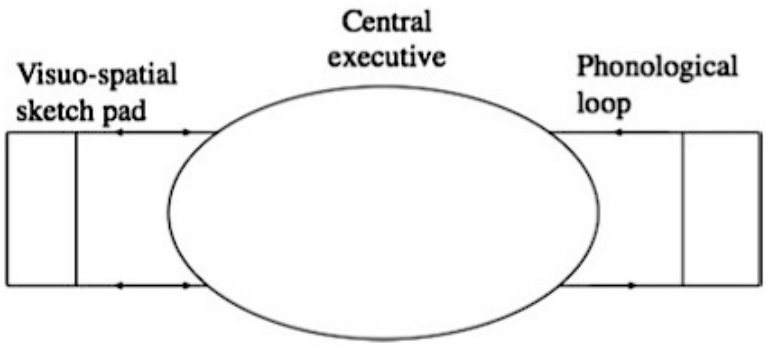


Figure 1-1: the original Baddeley and Hitch (1974) multicomponent model of working memory. *Note*. Reprinted from "Working Memory: Theories, Models, and Controversies" by Baddeley. A, 2012, *Annual Reviews of Psychology* 2012:63,1-29.

The third subsystem refers to the visuo-spatial sketchpad, a memory system to manipulate and store both visual and spatial content. Nevertheless, after the formulation of the original multicomponent model of WM, researchers showed that visual and spatial information are slightly disentangled between different systems. Studies on visuo-spatial memory using different versions of the Corsi block-tapping test have showed that visual features such as colours, but not spatial information (e.g., coordinates in space) decrease recall of visual information and *vice versa* (Milner, 1971). Furthermore, neuropsychological evidence indicates that some patients are exclusively impaired in memory maintenance of either visual or spatial information (Della Sala et al., 1999; Darling et al., 2006; Klauer and Zhao, 2004).

Overall, since its original proposal, the multicomponent model of WM has been revisited, challenged, and expanded. Newer proposals suggest additional systems to deal with a wider range of stimuli that seem to differ in the nature of the information to be stored (Fig.1-3). Specifically, the existence of a WM system has been proposed to hold in memory body-related information such as body movements and tactile information. Here, body-related information would be encoded in a body-related system that goes over an above other memory systems. This information would be

encoded and stored in a body-related system because the nature of the information (bodily) is conveyed in the percept regardless the type of acquisition (Fig. 1-2) (*this matter will be expanded later in the chapter*).

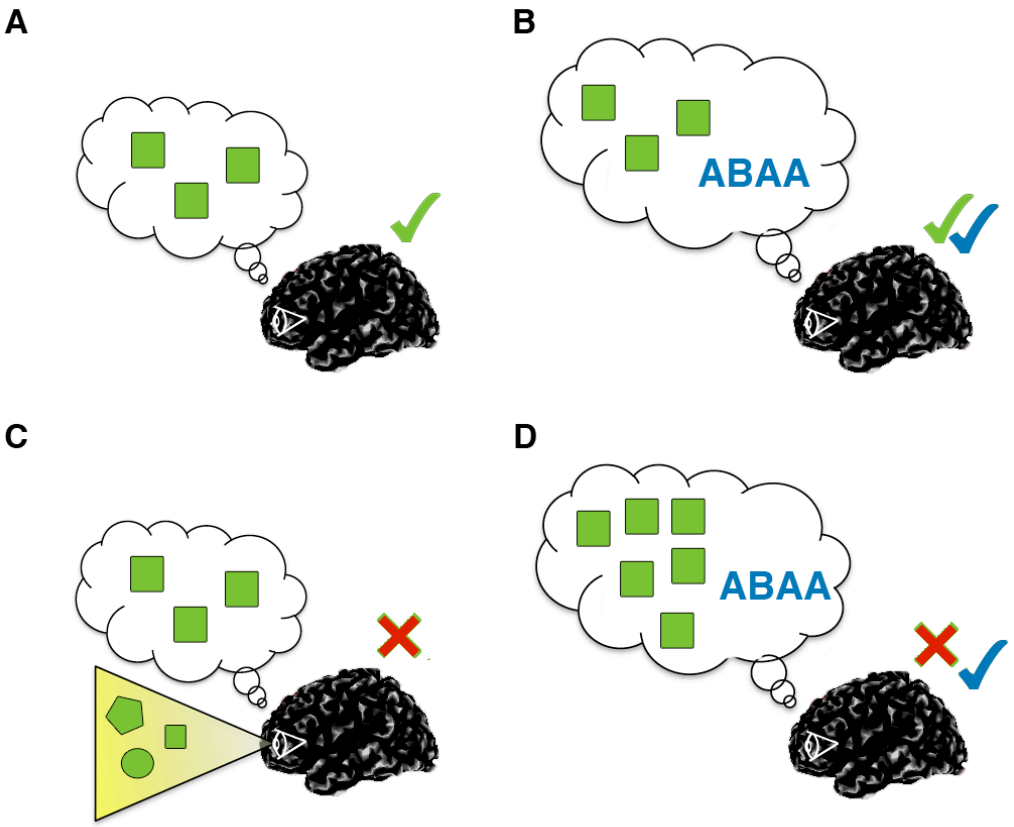


Figure 1-2: Schematic illustration of storage in specialized systems of limited capacity. ***A***, successful maintenance of three visual items in the visual sketchpad. ***B***, successful maintenance of visual and semantic items in visual and phonological loop, respectively. Since the items do not belong to the same category/nature, these are correctly encoded and maintained in independent WM storages. ***C***, dual tasks that require the visual sketchpad, such as holding in memory visual stimuli and perceiving additional visual events, disable the visual memory process by exhaustion of resources that otherwise could be allocated to memory maintenance. ***D***, increasing memory load of the same stimuli category (visual items) leads to poor memory performance during recall of visual items. Conversely, this process does not overload other memory systems, leaving enough workspace for the correct recall of other non-related visual items (e.g., semantic)

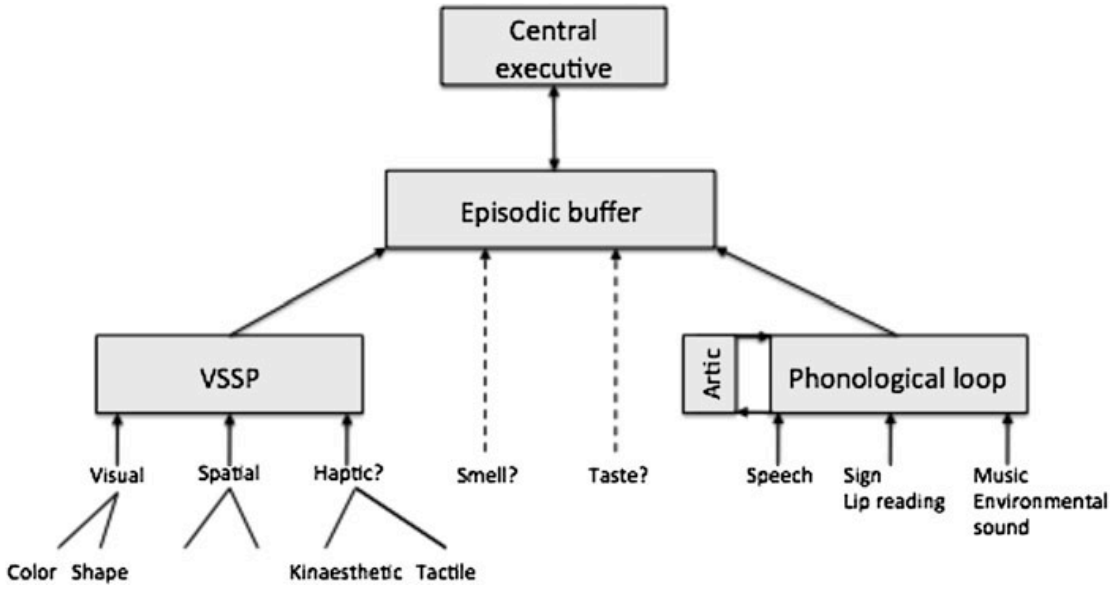


Figure 1-3: Hypothetical flow of information between perception and WM. VSSP, visuo-spatial sketchpad. *Note*. Reprinted from "Working Memory: Theories, Models, and Controversies" by Baddeley. A, 2012, *Annual Reviews of Psychology* 2012:63,1-29.

To this point, three important ideas need to be considered: i) WM is underpinned by several systems that are limited in capacity, ii) these systems are specialised in processing distinct types of information, and iii) these systems have been delineated by asking participants to perform suppression tasks that aim to disrupt the usual course of the memory trace. If these suppression tasks include computations or stimuli that require the same mechanisms needed to successfully encode and recall the stimuli to-be-remembered, decreasing memory performance is be observed (e.g., exposing participants to additional semantic information while remembering words).

1.1.2. Sensory recruitment during WM: link between perception and memory

The neural underpinnings of WM are usually examined while participants recall differences between a briefly presented memory phase, containing the stimuli to-be-remembered, and a test phase that differs in 50% of the trials (i.e., delayed matching-to-sample tasks). While doing this, a distributed network of brain regions that

comprises prefrontal cortex (PFC) and more posterior modality-specific sensory areas are active. Specifically, brain activity during maintenance of stimuli in WM has been well described in PFC (Fuster and Alexander 1971; Romo and Salinas 2003; Kostopoulos et al. 2007). The dorsolateral PFC assists with the maintenance of information by directing attention towards internal representations of sensory stimuli, which seem to be stored over more posterior areas of the brain (Curtis and D'esposito, 2003). These latter regions include sensory areas such as visual, somatosensory, and auditory cortices. Importantly, these brain regions do not only play a role during the perceptual stage but also during memory encoding. For instance, visual cortex and associated cortices seem to have a role in the acquaintance, perception, and maintenance of visual stimuli in memory (Becke et al., 2015; Tood and Marois, 2004). The correspondence between sensory-input modality and the neural underpinning for the maintenance of stimuli in WM is similarly observed across modalities such as tactile (Zhou and Fuster 1996; Kaas et al. 2013, Katus, Grubert and Eimer, 2015) and auditory (Arnott et al., 2005).

1.1.2.1. Persistent sensory activity during WM processing

Increasing activity in brain areas with a role in perceptual processing has been observed between the presentation of the stimuli to-be-remembered and their recall (Fig. 1-4). For instance, Vogel and Luck (2004) showed how mean amplitude of EEG waveforms are modulated according to the number of coloured lines and squares to-be-remembered in a visual WM task. The authors showed how after a short presentation phase, when the stimuli disappeared, brain activity over posterior sites started to increase around 300ms after the onset of the stimuli, steadily increasing from memory load 1 to 4; load referring to the number of items to be remembered. The increase in mean amplitudes seemed to also correlate with the memory capacity of the participants and with the capability to handle the information. A follow-up paper

showed that compared to participants with low memory capacity, higher performers exhibited smaller increases in brain amplitudes, presumably reflecting less depletion of computational resources under similar tasks (Vogel et al., 2005).

The so called persistent, delayed, sustained, or suprathreshold activity is characterised by i) steady increases on brain activity that are concomitant to the number of items to-be-remembered, ii) the increase of this activity seems to correspond to participants' memory capacity and efficiency of the storage, iii) sustained activity seems to reach a plateau when participants' memory performance breaks down (when memory capacity is reached). iv) This activity can be observed through multiple techniques. For instance, using electrophysiological and neuroimaging paradigms (e.g., Vogel and Machizawa, 2004; Pessoa et al., 2002), in lesion studies (Bisley and Pasternak, 2000) by microstimulation in the monkey's brain (Bisley, Zaksas and Pasternak, 2001), as well as using intracranial recordings in the human brain (Axmacher et al., 2007). v) the corresponding activity usually takes the form of persistent activity during the consolidation of the information in WM, being affected by attentional shifts of attention and different types of sensory interference (Pasternak and Greenlee, 2005; D'Esposito and Postle, 2015). Importantly, vi) it is observed in those perceptual brain regions that match the sensory acquisition of the percept (i.e., visual cortices in visual WM tasks).

The very specific role of this persistent activity and its relation between attentional control and memory consolidation are still being investigated (e.g., van Dijk et al., 2010; Lewis-Peacock et al., 2012). Nevertheless, its sensory source and memory modulation have led to sensory recruitment models of WM (Pasternak and Greenlee, 2005; Postle, 2006; Sreenivasan et al., 2014; Postle, 2006; D'Esposito, 2007; D'Esposito and Postle, 2015; Serences et al., 2009). These models propose that WM is better characterize as a reestablishment of the perceptual stage, in which transient

maintenance of stimuli occurs in sensory cortices that also process these same stimuli in the absence of WM demands (D'Esposito and Postle, 2015; Tsubomi et al., 2013). Moreover, sensory recruitment models also postulate that brain regions with a role in perceptual processing develop in correspondence to long-term associations that reflect how information is treated in WM. Remarkably, the philosopher David Hartley articulated a similar proposal three centuries ago. He proposed that memories are linked to associations in the same regions of the brain that processed the original sensory experience.

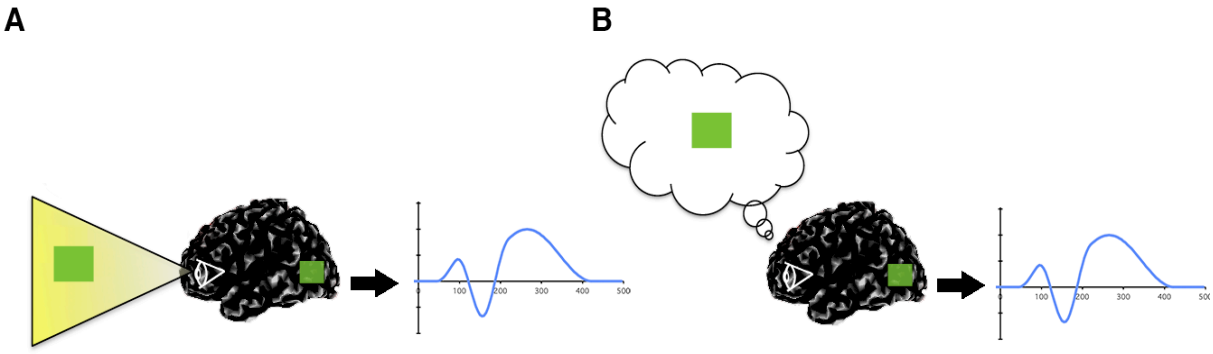


Figure 1-4. Schematic illustration of sensory recruitment models of WM in the visual domain. ***A***, perceiving visual information such as coloured polygonal shapes elicits brain activity in the visual stream, which is reflected by the concomitant EEG waveform plotted in blue. ***B***, encoding and maintenance of similar visual information in the absence of direct sensory stimulation also elicits brain activity in the visual stream, plotted again in the blue EEG waveform. In both cases, perception and WM maintenance, similar patters of brain activity can be observed, portraying a functional role of perceptual brain areas beyond the perceptual stage.

In conclusion, behavioural research in WM has delineated several non-overlapping systems that are specialised in processing different types of tasks and stimuli. More recently, neuroimaging studies have shown evidence of where and when in the brain this is happening. Brain areas playing a role in perceptual processing also hold the percept in WM. This has an essential impact in the way we understand brain

function, as well as and in designing new methods and paradigms. It also implies that brain streams that have been found to play a role in the perceptual domain are likely to also contribute to WM processing.

1.2. Working memory for body-related information

In the previous sections I outlined research accounts in the overall working memory field. Here I focus on WM processing for a particular set of stimuli: visually perceived body-related information such as body postures and actions. To this aim, I introduce what makes bodily stimuli so unique. Then, I review behavioural evidence for a specialised storage of sensorimotor information –related to bodies and actions. Third, I speculate about the neural candidates of such WM system. To this purpose, I consider two pieces of information: sensory recruitment models of WM (which postulate resemblance between perceptual and memory mechanisms) and studies on action observation.

1.2.1. Introducing the body as a percept to be remembered

Most of the studies that examine WM use arbitrary non-body-related stimuli. However, bodily stimuli such as images of body postures and actions possess specific features that differ from those that can be extracted, recoded, and later accessed from non-body-related stimuli. These fundamental differences are summarized in the following points/paragraphs.

(1) The majority of WM studies use participants' recognition to test memory performance. Specifically, at the end of the trial, participants are asked to detect differences between the memory and test stimuli/displays (e.g., in delayed matching-to-sample tasks). However, in WM studies using visually perceived body-related information, memory performance can be tested by asking participants to recognize differences between visual stimuli/displays or by asking them to actively execute the

percept to be remembered. For instance, a given paradigm may ask participants to detect differences between visual displays of actions or ask the participants to perform the actions studied during the memory phase. (2) The first point highlights how in WM for bodily information, a shared container of reference (the body itself) is common to the origin and source of the memory and the observer. (3) In memory for non-body-related information all stimuli can be accessed at once. (i.e., encoding all stimuli in a single display). Conversely, numerous body-related stimuli such as actions are generally accessed in serial order, one at the time. In other words, there is only one representation and corresponding execution at a time, with transitions between movements in a discrete hierarchically-organized and goal directed manner (Endress and Wood, 2011). (4) Stimuli such as body postures, movements, and actions are dynamic. They involve either arbitrary and intransitive pattern or well-defined configurations of movements. Moreover, processing of body form (patterned postures) and body movements (fluent moves) seem to follows slightly different memory routes. Vicary and colleagues (2014) showed how recognition of patterned and fluent body movements specifically interfere with patterned-based and motion-based interferences, respectively. (5) The characteristics of body-related stimuli are defined by the goal of the actions conveyed in the visual percept. When perceiving body movements to-be-remembered, for instance, hand movements to spatial targets can be done with more than one effector. Other examples require specific configurations of the body (e.g., performing an arabesque) (Smyth and Pendleton, 1989). Therefore, bodily stimuli can be encoded at distinct levels, from more abstract (an action regardless the specific kinematics) to more specific (a very specific type of action). (6) Visual stimuli depicting body postures, movements, and actions convey information that can be independent of temporal and spatial coordinates. They can exist in different times and locations in space, in a similar time but in different

locations, as well as, in identical locations at different times. Recognising these parameters in the actions would depend on additional information that, contrary to memory for non-body-related information, body postures and actions may convey. Specifically, contrary to memory for non-body-related stimuli, bodily ones can convey specific agents for specific bodily stimuli (e.g., memorising actions depending on specific agents).

1.2.1.1. Behavioural evidence for a separate WM system for body-related information

In the following sections I review behavioural studies that support the existence of a WM system dedicated to encode and maintain visually perceived body-related information. As for the aforementioned WM systems (e.g., visuo-spatial sketchpad and phonological loop), the present system has been mostly delineated by the use of interference tasks (note that since *Chapter 5* includes three experiments specifically using interferences/suppression tasks, a table summarizing all studies using interferences can be found in *Chapter 5, table 5-1*). Last, as noted in the previous section, WM for bodily stimuli can be studied via paradigms examining memory performance by action reproduction or action recognition, hence the following studies are presented according to this classification.

1.2.1.2. Memory for actions reproduction

Researchers have studied memory for action reproduction by asking participants to observe/encode, maintain, and reproduce actions in serial order. Moreover, as in previous WM studies, these tasks are used in the context of dual tasks paradigms, in which the aim is to examine whether specific memory processes can be concurrently performed with another task. Precisely, Smyth and colleagues (1988; 1989) asked participants to perform two WM conditions, one in which participants had to remember different numbers of body movements, and a second condition in which they had to

remember movements to specific spatial locations. At the same time, participants were also asked to perform two concurrent tasks: a movement suppression task and a spatial suppression task. The results showed a interaction between memory performance in the memory tasks and the type of suppression task. Specifically, memory span for body movements was significantly impaired by alternating configurations of the participants' hand (i.e., movement/sensorimotor suppression) but not by a spatial suppression task performed with the same body part. Conversely, memory span for spatial locations in space was significantly affected by a spatial suppression task. These early studies suggested the presence of a WM system dedicated to maintain body-related information, which can be dissociated from a more specialised system for spatial information about locations.

Later studies replicated the dissociation showed in the studies of Smyth et al (1988; 1989). Precisely, in the first experiment of Woodin and Heil (1996) participants were asked to remember body configurations adapted from Smyth et al. (1988) and location in space using the Brooks tasks (Brooks, 1967), which consists in holding in memory a set of numbers and their relative spatial locations within a matrix (e.g., place 3 in the lower right corner, then place a 2 above this position). Then, participants were instructed to perform two suppression tasks aiming to disrupt visuo-spatial memory and body processing, a square tapping task and a body-tapping task. Results showed that memory span for spatial locations in the Brooks task decreased when accompanied by the square tapping whereas span for body configurations diminished when concomitant to body tapping. Further studies have also found double dissociation between spatial and sensorimotor processing. Rumiati and Tessari (2002) tested participants to remember pantomimes of object-related actions during articulatory, motor, and spatial suppression. The authors found that motor and spatial suppression could be dissociated even when both types of suppression

required similar amount of cognitive resources. In other words, dissociation between motor and spatial storage for actions was delineated by the use of suppression tasks that in principle were equally demanding. Hence, their results are unlikely to be due to dissimilarities in the difficulty of the suppression tasks.

Other studies have been designed to take advantage of long-lasting associations, built through body experience, and their effects in WM processing. Cortese and Arnau (2010) asked ballet dancers to encode different ballet movements while performing motor or spatial suppressions tasks. The results showed that memory performance for ballet movements was affected by the motor suppression task, whereas memory for the locations in the stage in which the movements had to be done was affected by the spatial suppression task. A more recent study has shown that body experts and non-experts also differ in the use of verbal and sensorimotor processing. Moreau (2013) tested wrestlers and non-experts to remember full body stimuli displaying movements of arms and legs during concomitant articulatory or motor suppression. The results showed that non-experts relied more in verbal codes, and that overall, body experts did better than non-experts (i.e., during the non-suppression and verbal suppression conditions). However, motor suppression affected experts' performance to the point that the advantage of expertise was completely nullified.

Interestingly, not only is memory for body-related information affected by a number of body-related computations such as body movements, but also movements themselves seem to be affected by memory processes associated with processing visually perceived bodily input. The second experiment of Woodin and Heil (1996) showed how different stages of a continuous body movement were disrupted by the memory encoding of specific types of information. The patterned phase of the participants' continuous movement was disrupted when observing and remembering the body configurations used in the aforementioned studies of Smyth and colleagues.

1.2.1.3. Memory for actions recognition

In the aforementioned studies there was an overlap between the encoding of body-related information and the active use of the body to disrupt the memory processing of such information (i.e., the use of the body in both stimuli and suppression tasks). Could the effects described in those studies be due to such overlapping? Smyth et al. (1990) showed that memory for visually perceived body configurations is disrupted by just observing other's actions during the retention period in which body movements are being maintained in memory. Moreover, other bodily computations such as holding a second set of movements and copying others' actions also decrease memory span for body movements. The latter example is remarkable because even when body movements were used as a filler task, in the absence of WM demands, they were still interfering with the recall of the body stimuli to-be-remembered.

In other studies, participants have to detect differences between different displays of body postures and respond to this task in the absence of execution. Furthermore, at the same time they are also asked to hold visual and spatial information of non-body-related stimuli such as arbitrary objects (i.e., colours squares). In 7 different behavioural experiments Wood (2007) showed that maintaining these later stimuli did not disrupt memory span for body postures. Conversely, WM for body-related stimuli is disrupted by having to remember serial information. For instance, when body postures and objects are sequentially displayed and the task implies serial maintenance, memory performance is affected (Smyth and Pendleton, 1990; Woodin and Heil, 1996; Wood 2007; Vicary et al., 2014). The mechanisms dedicated to sensorimotor information could support also other types of non-body-related sequential information (Wood 2007; Schubotz 2007).

1.2.1.4. Capacity limits in body-related WM

Support for a separate storage for sensorimotor memory also comes from delineating the mnemonic capacity of its underpinning system. While researchers still investigating the exact mechanisms limiting our memory capacity (Ma, Husain, and Bays, 2014; Constantinidis and Klingberg, 2016), there is general agreement on our highly limited capacity of storage. Only three or four simple visual stimuli can be held in memory (Luck and Vogel, 1997), and others found that even less can be stored if these possess greater load of information (Alvarez and Cavanagh, 2004). For actions, only between two and three are well maintained in working memory (Wood, 2007; Wood 2008; Wood, 2011; Smyth 1990; Smyth 1988, Gao, Bentin and Shen, 2014). However, nine sensorimotor properties (i.e., type of action, body side, and duration) distributed across three body actions can be remembered as well as three properties across three actions (Wood 2007). These studies also show that when encoding actions in addition to other non-body-related features, participants' performance decline. For instance, maintaining in memory the agent, point of view, and background scenario of specific actions decreases memory performance (Wood 2008; Wood 2010; Urgolites and Wood, 2013, respectively). Thus, similarly to visual WM for simple objects, where binding a conjunction of visual properties does not translate in a big loss of capacity storage (Luck and Vogel, 1997), binding properties inherent to body actions in working memory seems to require little computational effort. On the other hand, if these are not body-related, additional computational processing is needed to bind information that probably belongs to different working memory storages.

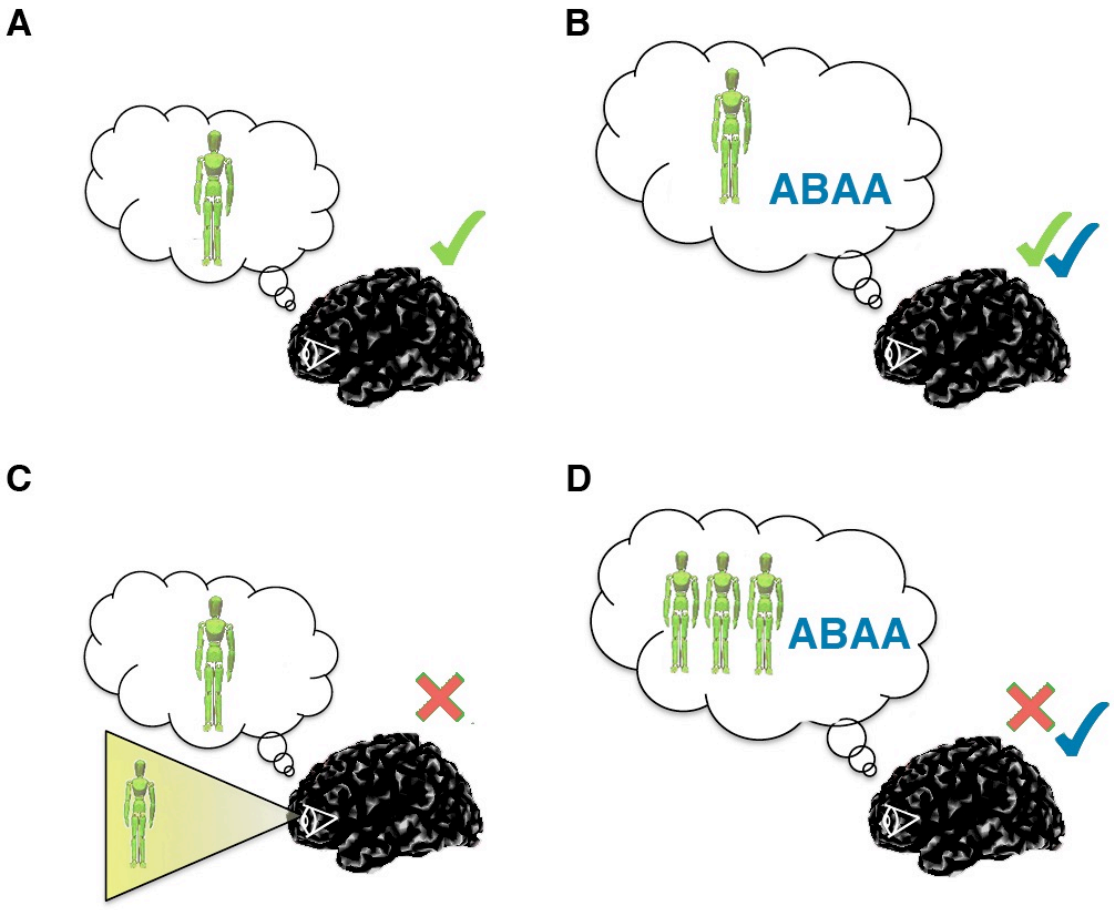


Figure 1-5. Schematic illustration of body-related storage in a specialized WM system of limited capacity. ***A***, successful maintenance of a single body-related stimulus in WM. ***B***, successful maintenance of a single body-related stimulus and semantic information in WM. Since this information does not belong to the same category/nature, stimuli are correctly encoded and maintained in supposedly independent WM storages. ***C***, tasks that require use of the body-related WM system, such as perceiving bodily events, disable such a system by exhaustion of resources that otherwise could be allocated to memory maintenance. ***D***, increasing memory load of the same stimuli category (bodily items) leads to poor memory performance during recall of body-related information. Conversely, this process does not overload other memory systems, leaving enough workspace for the correct recall of other non-related bodily items.

1.2.1.5. Wrapping up behavioural evidence of a specialised WM system for body-related information

Considering the compound of studies included in this section, it is possible to postulate the existence of a WM system dedicated to encode and maintain body-

related information. In dual-task paradigms, this system (or subsystem) is not impaired by memory or perceptual tasks that use non-body stimuli (i.e., colours, matrices, words). Moreover, it is engaged whether memory for actions is tested in delayed matching tasks or in paradigms asking participants to actively perform the actions to-be-remembered, that is, the mechanisms behind this WM system seems to be driven by the nature of the information conveyed in the percept (i.e., supramodal). Crucially, the consolidation of visually perceived body-related information seems to be overloaded by adding sensorimotor-like load to the visual display (i.e., quantity of body-related information conveyed in the visual display) or by using one's sensorimotor system during movement/motor suppressions. Altogether, there is behavioural evidence for a WM system for body-related information, the neural underpins which seem to exist on our own body representation in the brain.

1.2.2. Neural candidates for a WM system to encode body-related information

To our knowledge there are no studies investigating how and where in the brain perceived bodily information is encoded and maintained during WM. Yet, it is possible to speculate with a certain confidence about the neural candidates for such processes. Here, there are three important pieces of information that need to be considered: (1) as I outlined in the previous sections, sustained activity that increases with memory load has been observed in sensory areas during WM tasks. Precisely, sensory recruitment WM models postulate that perceptual brain areas also play a key role in memory processing (D'Esposito and Postle, 2015). Nevertheless, these findings have been found in studies mostly using non-body-related stimuli. (2) Behavioural studies in WM for visually perceived actions suggest that similar specialised mechanisms underpin the perception of others' bodies, as well as one's sensorimotor processing (namely, similar brain areas that we use to move and feel

our own body). Last, (3) there are a large number of studies that have studied perception of others' bodies and actions; showing that our own body in the brain plays a crucial role in perceiving such bodily interactions. Altogether those three points concatenate into the following idea: neural candidates for a WM system to process body-related information are possibly those with a role in perception of bodies and actions. For this reason it is important to encapsulate these brain areas and their functions during action observation.

1.2.2.1. Brain regions known to have a role in body and action observation

Observing whole bodies activates the fusiform body area (FBA), the function of which differs slightly from the extrastriate body area (EBA), a brain region with neurons that fire when seeing specific body parts (Downing et al., 2001). Moreover, there is also the fusiform face area, which responds to the sight of faces. Note that findings about these brain areas suggest that face and body selective regions are closely related. As Gelder et al. (2010) suggested, it is possible that when seeing either faces or bodies, the brain fills the gap and recreates automatically the remaining bodily percept. Remarkably, visual perception of static bodies such as body postures elicits neural processing in brain regions usually associated with perception of complex motion (Kourtzi and Kanwisher, 2000) and motor regions (Urgesi et al., 2006). The engagement of regions linked to processing of dynamic influx during perception of static bodies suggests that the brain extracts fluency from snapshots.

Body movements convey information about the kinematics, the internal and external dynamics that act on the human body, and causes of the body to move in the way it does. When bodies are observed, the perceivers' brain engages a distributed network of neural regions that respond to those features; the widely known mirror system, located over our own motor system responds to somebody else executing actions. Originally discovered in the area F5 and PF of the macaque monkey, mirror neurons

discharge when an action is either executed or observed (di Pellegrino et al., 1992; Gallese et al., 1996). Despite the cytoarchitecture and function of these neurons being still controversial, many studies have reported mirror-like activations in the human brain (Mukamel et al., 2010). Interestingly, despite bodily information being initially perceived through different sensory modalities, further mirror activations take place over sensorimotor and somatosensory brain areas. EEG studies using sounds of actions elicited larger mu rhythm suppression, a neural marker of sensorimotor processing, over the contralateral hemisphere to the dominant hand when compared to hearing control sounds (Pineda et al., 2013).

Brain regions with mirror properties (i.e., vPMC, dPMC, IPS, S1) (Fig. 1-6) and the more posterior and ventral regions (posterior parietal and occipitotemporal) regions comprise the action observation network (AON). The AON includes several structures of brain systems partially overlapping and contributing to both perception and execution (Kilner, 2011), and more specifically, functions related to visuomotor processing and acquisition of motor skills (Sakai et al., 2002; Grèzes et al., 2003). Altogether, AON is modulated by sensorimotor experiences that are acquired over time, that is, a form of long lasting association linked to both perception and execution of a particular set of actions. For instance, learning new body movements enhances parietal and premotor cortices; areas known to participate in perception of others and one's own motor acts (Cross, Hamilton and Grafton 2006; Calvo-Merino et al., 2005). The patterns of activity within these regions vary depending on how body experience is gained (e.g., just by seeing actions and/or by actively engaging in learning actions) (Calvo-Merino et al., 2006; Cross et al., 2009).

More recently, connectivity analysis has showed that participants' experience for body movements modulates reciprocal attenuations between parietal and more posterior cortices (Gardner et al., 2015); areas of the brain involved in the processing

of body image and visual input, respectively. Furthermore, machine learning techniques and fMRI data have revealed that brain regions typically associated to motor production and posterior additional sensory areas code actions at different levels. Inferior parietal and occipitotemporal lobes code actions at abstract levels. Contrariwise, premotor cortex seems to code actions at the more concrete level. This latter finding implies that posterior brain areas carry an important weight in understanding the observed actions (Wurm and Lingnau, 2015).

Figure 1-6. Schematic illustration of brain regions usually reported in studies of action observation. EBA: extrastriate body area; S1: primary somatosensory cortex; IPS: instraparietal sulcus; vPMC: ventral premotor cortex; dPMC: dorsal premotor cortex; SMA: supplementary motor area.

1.3. Putting it all together: WM system for visually perceived body-related information (summary)

Human interaction implies observing, learning, and reflecting about others' bodies, movements, and actions. This requires perceiving and encoding bodily information acquired through our senses and its later transformation into internal body representations that can be later retrieved from memory —memories related to bodily information. By doing this, we go from mere sensory input to functional and meaningful cognition that allows us to recognize, understand, imitate, and learn from

others.

Memory systems comprise several systems specialised in processing different types of information and subsequent tasks. There is good evidence for the presence of visuo-spatial and phonological systems handling visuo-spatial and semantic information. More recently, another system for the encoding and maintenance of visually perceived bodily information has been suggested (Baddeley 2012). The neural regions engaged in the latter system are largely unknown, however, behavioural studies suggest that our own cortical representation of the body in the brain may play a role in memory for observed actions and body postures. Importantly, contemporary models of WM postulate that brain areas contributing in perception also support WM storage. Therefore, it is possible to theorise that brain regions known to participate in perception of body stimuli also contribute to holding in WM these stimuli. Precisely, imaging, electrophysiological, and direct recording of brain activity have shown that a distributed network of brain areas known as the action observation network (AON) is engaged during perception of bodies. AON includes posterior sensory-input regions that 'receive' visual percepts of actions and static body postures, as well as more anterior cortices that are relevant for the perceivers' body movement and sense of touch (i.e., sensorimotor and somatosensory cortices).

Therefore, the WM system for encoding and maintenance of visually perceived bodily input is probably overlapping the regions of the AON. Considering the behavioural evidence revised before (e.g., Smyth et al., 1988,1989,1990; Cortese and Rossi-Arnaud, 2010) such overlap is probably arising over sensorimotor and somatosensory regions. Thus, brain areas contributing to body perception are likely candidates to store visual bodily percepts. This framework provides additional systems tightly linked to action and bodily perception with functional properties

related to memory cognition. Nevertheless, it remains unclear if body-related cortices are involved (beyond perception) in maintaining body stimuli to-be-remembered in memory. Here, several specific research questions arise:

1.3.1 Research questions

Experimental/theoretical questions:

- Does the sensory entry modality or the nature of perceived information (body vs. non-body-related) dictate where in the brain information is processed and maintained in WM?
- Is our own body representation over sensorimotor cortices maintaining body-related percepts in WM beyond the perceptual stage? (i.e., encoding and active maintenance of bodily stimuli when these are not within direct view).
- Do distinct body-related brain areas (motor and somatosensory cortices) participate in the encoding and maintenance of body stimuli? And how are these dissociated from the concomitant visual processing of body images?
- What is the causal role of these body-related body areas in the brain during maintenance, consolidation, and retrieval of the stimuli to-be-remembered and how are these detached from other types of sensory information?

Technical/methodological questions:

- How can we dissociate brain activity arising from body-related regions and sensory-input regions such as visual cortices? (while preserving high temporal resolution).
- Given that previous studies have shown that somatosensory and sensorimotor cortex support the perception of bodies and actions, how can we explore the discrete contribution of these areas from concomitant visual activity?

1.4. Artistic Impressions I

Visual Realm - Merged landscapes: Vision I – VI (2015) Photography on board (21 x 21cm) / AGP. Colours, luminance, contrasts, and shapes provide an immeasurable part of our vivid phenomenological experience. Countless memories are built though vision. This collection contains two elements: (1) Visual textures and colours embedded in the models' head in those posterior areas where research has showed that visual information is held (landscapes were taken in the Serra de Tramuntana, Mallorca. World Heritage Site). (2) Parts of the models' heads are covered by their hands. This occlusion is not arbitrary. My PhD work seeks to understand how these regions could hold other types of memories such sensorimotor (—related to body movements and actions).

2. Chapter 2: Revealing hidden representations of the body in the brain

An important part of the work presented in this thesis is theoretical, as well as purely methodological. This is partially due to the complexity of my object of study: the body, as a percept to be remembered it embraces experimental and conceptual challenges that are present in both action observation and memory fields.

In this second chapter, I first present a very short introduction to electrophysiological recordings. Secondly, I consider how further paradigms need to consider processing of body-related stimuli as a very particular set of neural processes/responses. Third, I revise, expand, and propose a novel EEG paradigm that aims to dissociate visual and somatosensory processing during encoding of visual bodily stimuli. Fourth, I outline methodological aspects that need to be considered in this paradigm and other EEG studies that examine neural responses associated to perception of body stimuli. Altogether, when considering the points developed in this chapter (and by considering how EEG works), it is possible to create new approaches that have the potential to explore with high temporal resolution the involvement of body-related cortices when seeing and encoding bodily-related information.

2.1. Basic foundations of EEG recording

2.1.1. Measuring EEG activity

Extracellular field recordings are the result of superimposed electric fields that originate in those electric currents generated by active neurons (Fig. 2-1). Initially, any of the excitable membranes found between neuronal elements (i.e., axons, dendrite, soma, and so on) build up a voltage difference in both the intra- and extracellular space (Murakami et al., 2002, 2003; Murakami and Okada, 2006).

Depending on the cytoarchitecture of the neural generators (e.g., properties of the tissue and alignment of neurons) the electrical fields created by the voltage deflections of numerous thousands of postsynaptic potentials enable the recording of brain activity by using different techniques such as electroencephalogram (EEG) (for further details on origins of extracellular recordings see Buzsáki et al., 2012),

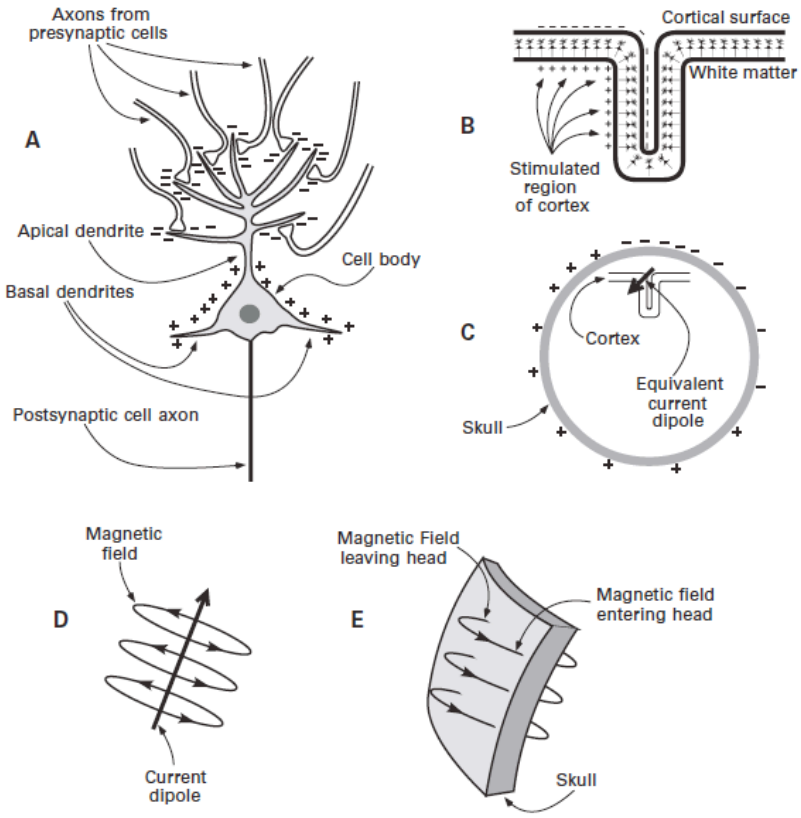


Figure 2-1. Principles of ERP generation. ***A,*** Schematic pyramidal cell during neurotransmission. An excitatory neurotransmitter is released from the presynaptic terminals in the apical dendrite, causing positive ions to flow into this region of the postsynaptic neuron. This creates a net negative extracellular voltage (represented by the " – " symbols) just outside the apical dendrite. To complete the circuit, voltage will flow through the neuron and then exit in the region of the cell body and basal dendrites (represented by the " + " symbols). This flow of current forms a small dipole. The polarity of this dipole would be inverted if an inhibitory neurotransmitter were released rather than an excitatory neurotransmitter. It would also be inverted if the neurotransmission occurred at the cell body or basal dendrites rather than at the apical dendrite. ***B,*** Folded sheet of cortex containing many pyramidal cells. When a region of this sheet is stimulated, the dipoles from the individual neurons summate. ***C,*** The summated dipoles from the individual neurons can be approximated by a single equivalent

current dipole, shown here as an arrow. By convention, the arrowhead indicates the positive end of the dipole. The position and orientation of this dipole determine the distribution of positive and negative voltages recorded at the surface of the head. ***D,*** Example of a current dipole with a magnetic field traveling around it. ***E,*** Example of the magnetic field generated by a dipole that lies just inside the surface of the skull. If the dipole is roughly parallel to the surface, the magnetic field can be recorded as it leaves and enters the head; no field can be recorded if the dipole is oriented radially (perpendicular to the surface). *Note:* Reprinted with permission from "An Introduction to the Event-Related Potential Technique, 2nd edition" by Luck, S.J. 2014, MIT press.

After a session of EEG recordings, the neural responses to the events of interest are averaged together. In the particular case of event-related potentials (ERPs), the averaging of the signal also includes non-specific brain activity, however, averaging the neural responses locked to a particular event across many trials averages out event-unrelated brain activity while including/enhancing consistent and task-related neural responses (Glaser and Ruchkin, 1976; Luck, 2014). In a very ideal world this would be enough to examine scalp potentials. However, extracellular field recordings such as ERPs measured by EEG are spatiotemporally smoothed (Niedermayer and Lopes da Silva, 2005; Buzsáki et al., 2012). In particular, the spatial resolution of EEG, this is to say, from where in the brain the observed brain activity arises, is still a challenging issue

2.1.2. ERPs - signal processing

The ERP components described in the ERP literature refer to neural signals that are generated in specific brain regions when performing certain mental computations. These components are recorded at the scalp and exhibit the sum of numerous underlying components, namely, there is a superimposition of components arising from multiple sources. Therefore, the slopes and peaks observed in EEG waveforms reflect the sum of several and distinct neural sources. The mixture of components contributing to these superimposed waveforms in scalp potentials is the so-called

'hard problem' that affects spatial resolution and the estimations of the neural generators of the signal (Cohen, 2014; Luck, 2014). Moreover, usually many neural generators are active and their superimposed patterns of signal may cancel each other. This cancellation decreases the overall observed signal that is averaged against noise (i.e., against task-unrelated and non-specific activity). Additionally, the percentage of voltage that is propagated from within different brain regions also varies depending on the underlying brain tissues and across electrode positions (Ahlfors et al., 2010; Irimia et al., 2012; Tenke and Kayser, 2012). Contrary to functional magnetic resonance imaging (fMRI), in which relevant modulations can be observed without superimposed and propagating signals across independent and largely distributed voxels, superimposition and propagation across scalp potentials result in important constrains. The loss of relevant information regarding the original time course and neural source of the signal needs to be considered.

Nevertheless, the temporal resolution of ERP-EEG is excellent, a matter that need to be considered when studying the very fast influx and processing of information in the brain. Components that peak as early as 20-40ms after stimulus onset can be already observed and documented (Urbano et al., 1997; Giard and Peronnet, 1999). This high temporal resolution is particularly relevant to compare mental chronometry across different populations and in examining the effects of experimental manipulations across conditions. Moreover, some of the problems regarding the superimposition of components can be overcome, not only by cutting edge implementations with already existent methods, but also by standard procedures. For instance, when examining ERP waveforms from various electrodes, the components across the scalp are quite similar but the contribution of each one of these across the observed electrodes actually differs (Fig. 2-2). Then, it is possible to picture the contribution of the components by comparing waveforms across both time and

electrode sites (Kappenman and Luck, 2012). Also, a paradigm that is based in well-supported evidence enables to make solid inferences when approaching the data, from where and when a component may be found to its hypothetical interpretations and neural underpinnings.

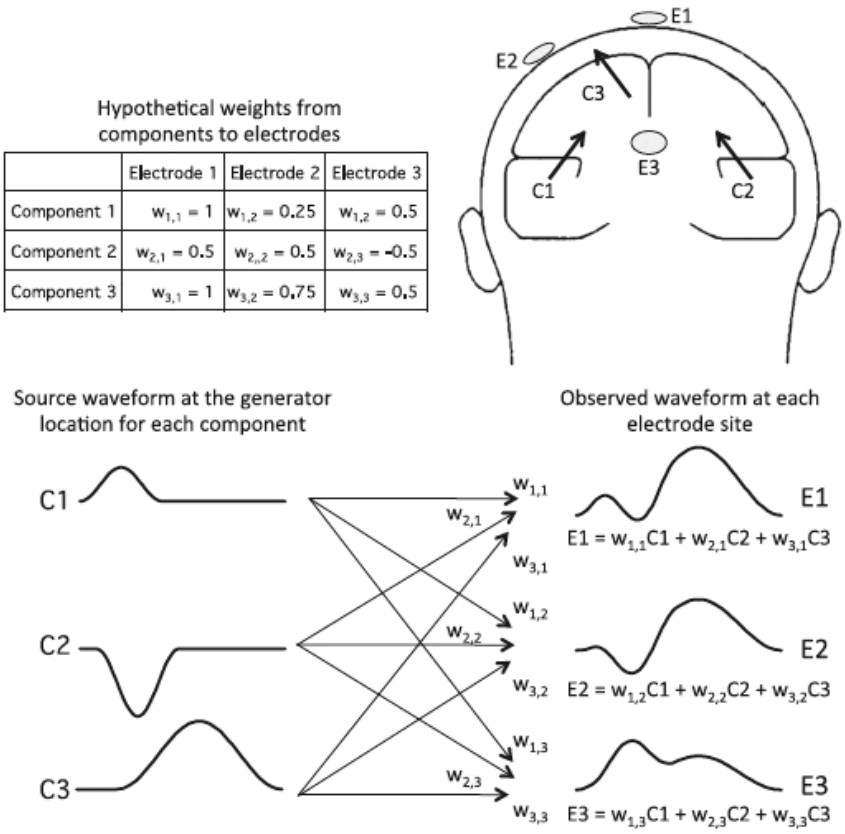


Figure 2-2. Relation between the underlying component waveforms and the observed scalp waveforms. In this example, three components are present (C1, C2, C3), each of which has a source waveform (time course of voltage, shown at the bottom left) and a generator location (represented by the arrows in the head). The contribution of each component waveform to the observed waveform at a given electrode site is determined by a weighting factor that reflects the location and orientation of the generator relative to that electrode, along with the conductivity of the tissues that form the head. The table shows the weighting factors between the three components, and the three electrode sites are given in the table (but note that these are made-up values, not the actual weighting factors from a real head). The observed waveform at a given electrode site (shown at the bottom right) is equal to the sum of each of the component waveforms, multiplied by the weighting factor between each component and that electrode site. The weights are indicated by the *w's* on the arrows between the

component waveforms and the observed waveforms (e.g., $w_{2,3}$ represents the weighting factor between component 2 and electrode 3). *Note:* Reprinted with permission from "An Introduction to the Event-Related Potential Technique, 2nd edition" by Luck, S.J. 2014, MIT.

2.2. Adapting ERP-EEG to explore the body in the brain

In many cases ERP studies focus on understanding general principles of human cognition by examining mental operations and subsequent waveforms that are concomitant to arbitrary stimuli. Yet, as revised in *Chapter-1,* when dealing with body stimuli, there are certain characteristics that need to be considered. Here we are referring to body-related stimuli in a broad sense. Nevertheless, distinct body stimuli recruit similar, as well as different neural mechanisms, for instance, processing bodies and faces exhibit some differences in the latency of ERP components and neural generators, as well as certain similarities when compared against non-body-related stimuli (for an excellent review on this topic see de Gelder et al., 2010).

Several aspects delineate how ERP experiments that use body stimuli need to be designed. (1) To start with and very briefly, one of the most important differences at the conceptual level is that processing body-related information such as visually perceived body parts (e.g., hand images) implies that similar vessel (the body itself) is shared between the observer and the percept. This factor is assumed to be crucial in driving sensory signals and computations about bodily percepts onto our own body representation in the brain (Niedenthal, 2007; Rizzolatti and Sinigaglia, 2010). The underlying process is different from any other non-body-related stimuli because they do not obviously convey such bodily-framed quality. Body stimuli elicit sensorimotor associations that have been developed by repeated sensory stimulation within and between one and others' bodies. Even when participants merely perceive body-related information and no action execution is required, sensorimotor associations —

related to bodily experiences, may play an important role (see for instance Calvo-Merino et al., 2005).

(2) A further factor that needs to be taken into account is the degree of 'bodily elicitation' conveyed in the experimental task. There is convergent evidence about the automaticity of body-related stimuli in driving embodied experience. Yet, factors such as the participants' body posture, action intentions, experience with the body stimuli to-be-encoded, instructions asking participants to explicitly attend non-body or minor body-related information in a bodily percept (i.e., gender of an actor or the colour of his/her clothing), and the perspective of the body stimuli within the visual field can both augment and reduce sensorimotor processing. An example of the latter instance can be observed when participants are asked to decide whether or not different objects are suitable for manipulation after brief presentations of hand images matching or not the posture of the perceivers' own hand. Matching egocentric primes result in faster RTs compared to non-egocentric ones, suggesting that the degree of overlapping between the effector and the body image facilitated the task (Jackson et al., 2006). From imaging data, another study reported greater activity in the left sensorimotor cortex for egocentric perception of actions than for non-egocentric (Bruzzo et al., 2008).

2.2.1. Considerations in the design of body stimuli

Overall, the properties of the stimuli affect their processing. Many experiments have shown that visual processing of body stimuli drives processing over and above very initial perceptual brain areas. Importantly, parameters of bodily elicitation have to be well controlled, since the number of trials needed to record ERP is normally larger than the those needed for behavioural experiments, it is not possible to manipulate extensively the parameters of the stimuli across trials and additional caution needs to be taken when choosing and designing the stimuli (Picton et al., 2000). On top of

that, since body-related information conveys multiple and parallel features, it is important to display unambiguous information. If we are interested on designing an experiment on how stimuli are processed depending on their nature (i.e., body or non-body-related), the difference between them needs to be clear and as far as possible well controlled. For instance, encoding of hand images that resemble objects or convey semantic information (i.e., specific hand signs and gestures) would confound the elicited brain responses and the subsequent recorded waveforms across the scalp. For instance, Gao et al. (2014) showed that instructing participants to verbally encode biological motion in points of light display portraying different bodily actions abolished mu suppression (an index of embodiment) compared to when participants were not prompt to explicitly use verbal codes.

2.2.2. Body *vs.* non body-elicited neural activity

Any ERP-EEG experiment will face a number of challenges that will obscure data interpretations, namely those briefly reviewed, signal propagation, its decay and cancelation, the presence of multiple and active neural generators, and the superimposition of observed components. Moreover, experiments examining body-related visual processing face an additional challenge: measuring ERP waveforms beyond those electrodes positioned over input-stimulated cortices, that is, measuring brain activity arising from cortex other than visual (e.g., central cortices such as somatosensory or more anterior as motor).

Specifically, visual perception of body-related stimuli recruits ‘sensory-input’ cortical regions (i.e., visual stream). This initial ERP visual signal is generally referred as visual-evoked potential (VEP), but it can be also found as visually-evoked response (VER) and visually-evoked cortical potential (VECP). Measuring VEPs over posterior/occipital electrode sites allows good measuring of activity directly linked to computations of the visual system during visual processing. For instance, EEG

studies examining attentional processes in visual search paradigms for colours and shapes report VEPs modulations over posterior electrodes sites; the location on the scalp where actual activity from the visual system is usually observed (e.g., Norcia et al., 2015). Electrodes over more anterior sites do not always reflect modulations of brain activity neither interactions concomitant to these basic visual tasks.

In addition to the visual cortex, the sight of body stimuli recruits sensorimotor, somatosensory, and other cortical regions across a distributed network of brain regions known as the action observation network (Calvo-Merino et al., 2006; Cross et al., 2006; Caspers et al., 2010; Molenberghs et al., 2012). The visually 'acquired' body percept is rapidly recoded over one's body-related cortices, which play a fundamental role in extracting, predicting, and performing computations related to others' bodies and actions, as well as one's sense of body movement. However, in EEG-ERPs studies the initial sight of body stimuli elicits the aforementioned VEPs that spread from posterior/visual to more anterior and body-related cortices, masking thenceforth the brain responses that are also responsible for the processing of body-related information. Therefore, encoding and other processes associated to the transformation of bodily information onto our own cortical body representation (i.e., sensorimotor and somatosensory) are difficult to tease apart from the VEPs linked to the signal delivering the visual percept. Measuring VEPs over posterior/occipital electrode sites allows good measuring of activity directly linked to visual processing but it does not facilitate direct inspection of the state of sensorimotor and somatosensory cortices. Consequently, the neural processes that are driven by the bodily nature of the information conveyed in the percept are difficult to dissociate from on-going visual signals.

2.2.3. Dissociating body-related cortical activity from visual concomitant generators

How can we measure and dissociate visual processing from ERP components arising from body-related cortices? Here we proposed a solution to probe the state of body-related cortices (i.e., somatosensory cortex) during visual perception of body stimuli in ERP-EEG experiments. This proposal involves four key elements: i) the use of stimuli that differ in the type of neural mechanisms that they evoke: body *vs.* non-body-related stimuli; alternatively this can be combined with the use of instructions that modulate the degree of bodily elicitation (e.g., attending actors' body postures *vs.* attending to actors' gender). ii) Eliciting ERPs 'delivering' visual body-related stimuli such as those VEPs elicited when seeing body stimuli. iii) Eliciting task-irrelevant ERPs over those cortical areas classically shown to be involved in processing of body stimuli. iv) The last step involves subtracting and comparing ERP components from multiple regions of interest and across conditions that manipulate the degree of bodily elicitation conveyed in the task. In the following sections these steps are described.

To illustrate how ERP components arising from body-related cortices can be dissociated from visual activity —VEPs, I revise and use as example a relatively recent study on *somatosensory involvement during perception of emotional faces.* Previous findings link our own somatosensory representation in the brain with perception of others' facial expressions (Pitcher et al., 2009). In order to dissociate somatosensory waveforms from concomitant visual waveforms elicited when seeing faces, Sel and colleagues (2014) used somatosensory-evoked potentials (SEPs) while participants' were observing faces with different emotional expressions. SEPs are obtained in response to brief cutaneous or transcutaneous stimulation, for instance, mechanical impacts on the fingertip, air puffs, and bipolar transcutaneous

electrical stimulation. These stimulations evoke ERP components in the contralateral primary and secondary somatosensory cortices (S1, SII). SEPs are a practical and non-invasive tool to assess the somatosensory system and its underlying processing.

In Sel et al. (2014) SEPs were elicited in 50% of the trials by delivering a task-irrelevant tactile tap either at the participants' face or index finger. These SEPs were always presented 105ms after onset of the images, which according to TMS studies, it is the timing needed for face images to be processed in somatosensory cortex (Pitcher et al., 2008). Therefore, half of the trials contained VEPs elicited at the onset of the images while the other half contained a mixture of VEPs also elicited when perceiving images plus those SEPs elicited at the onset of the tactile tap. The only purpose of the task-irrelevant tactile taps was to reveal the state of somatosensory cortices during visual processing of facial emotions (Fig. 2-3). This design allowed measuring source waveforms of somatosensory processing (SEPs) by subtracting brain activity from trials containing only VEPs to those VisualTactile trials containing a mixture of both VEPs and SEPs. By conducting the subtraction (VEPsSEPs — SEPs), the authors exhibited novel evidence of pure somatosensory processing modulated by stimuli driven-activity, seeing facial expressions, with fine temporal resolution. Importantly, in the control condition, participants were asked to attend to the gender of the faces. Once participants attended the visual features embedded in this task, the modulations of isolated SEPs were not found.

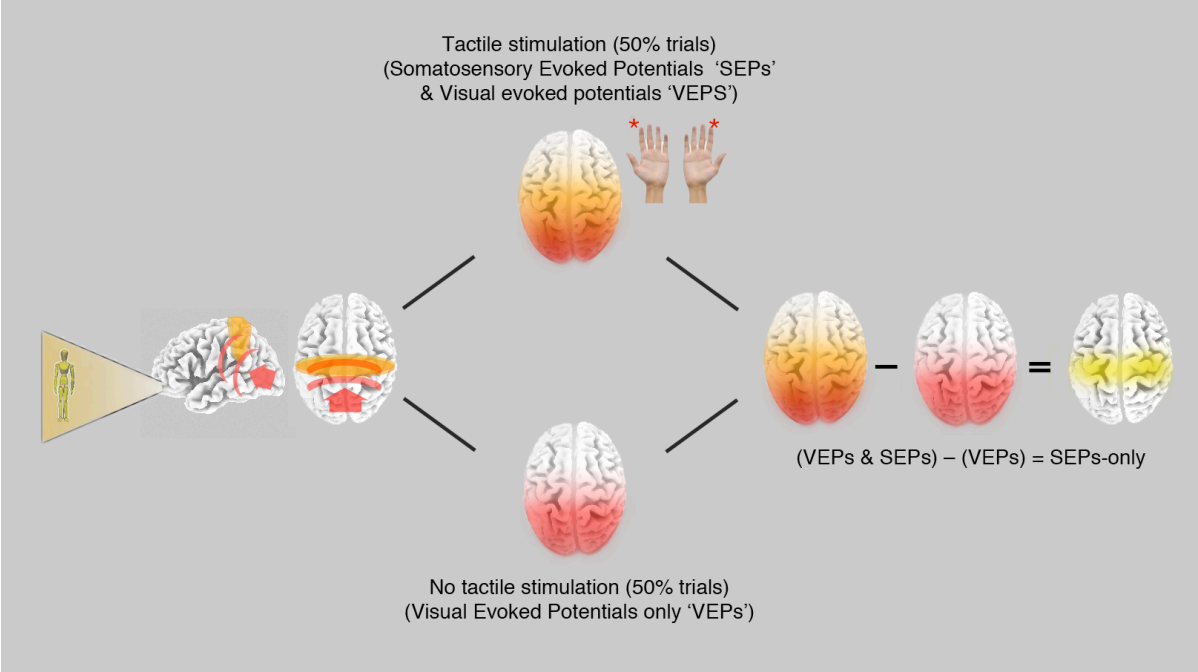


Figure 2-3. Schematic illustration of subtractive methodology using SEPs and VEPs. From left to right, perceiving bodily stimuli elicits visual-evoked potentials that conceal possible and concurrent processing in other regions such as somatosensory cortices. Next, in a given experiment, 50% of trials in include visual perception of body-related stimuli, which evoke VEPs (central-bottom part). The remaining 50% of trials include similar VEPs, as well as somatosensory-evoked potentials (SEPs) elicited by task-irrelevant tactile stimulation (central-upper part). The latter allows probing the state of the somatosensory cortices, which activity can be dissociated from visual activity in the subtraction illustrated on the right [(VEPs&SEPs) – (VEPs-only)].

In brief, the method behind the subtraction of VEPS to the ERP signal containing VEPs and SEPs is a well-known procedure that has been widely implemented in numerous EEG-ERP paradigms across different subjects of study. The idea is to isolate specific ERP components by means of difference waveforms, particularly, computing differential activity by subtracting ERP waveforms elicited by one condition from the ERP waveforms elicited by another condition. In the case of Set el al., (2014), these conditions would refer to the type of activity reflected on scalps by the single or combining elicited ERPs during perception of facial expressions. Seeing images of faces 'delivered' the percept while eliciting VEPs and task-irrelevant SEPs

were then used to explore cortical areas linked to body processing. Next, by means of subtraction it was possible to isolate neural processes that were differently exposed in both conditions while reducing brain activity equally present in both conditions. This procedure is very useful in disentangling components that otherwise are difficult to observe and isolate.

2.2.3.1. Types of subtractive-procedures

Subtractive methodologies vary in their scope and design. For instance, in some studies different operations are inserted in a sequence of cognitive processes. In cognitive subtractions, each individual step is thought to reflect those cognitive processes and neural activations that compose the whole (much like differences of mental operations in Donders' experiments) (Donders, 1868). Nevertheless, current postulates criticize the linearity of these types of subtractions, which neglect the interactions between cognitive processes and neural systems (Friston et al., 1996; Jennings et al., 1997; Price and Friston, 1997; Vidal et al., 2011).

Another type of subtraction that is closer to the one proposed is that commonly found in studies examining how information from different sensory modalities is integrated. In multisensory integration different stimuli are presented through two or mores sensory modalities in a synchronised or desynchronised manner. By subtracting brain responses to unimodal and multimodal presentation of stimuli, it is possible to dissociate waveforms that are likely to reflect sensory integration (Dell'Acqua et al., 2003; Talsma et al., 2010; Mahoney et al., 2015). However, there are at least two important differences between this latter type of subtractions and the one introduced in (Sel et al., 2014). In many studies of multisensory integration, audiovisual integration is examined by comparing trials containing waveforms elicited by either visual, auditory, or the simultaneous presentation of both stimuli types. Sensory integration is assessed by computing the difference waveform between brain

responses to the audiovisual condition and the sum of unimodal auditory and visual conditions (i.e., Audiovisual – (Audio + Visual). This is substantially different from the subtraction performed in (Sel et al., 2014) (i.e., VisualTactile – Visual). First, these two subtractions differ in the number of scalars and operations that they take into account; only a single operation is used in the latter subtraction. Secondly, in the latter study SEPs *per se* do not provide any information about the visual input. SEPs elicited by a task-irrelevant tactile tap can hardly convey any valuable information about the characteristics of external body-related percepts (e.g., seeing others' actions or body postures). Somatosensory responses to visually perceived body-related information do not explicitly reflect sensory integration but probably associations that summon processing resources (Meyer et al., 2011; Sun et al., 2016). This type of neural course is often invoked independently of intentional control; rather, stimuli salience drives the processing of information (e.g., seeing a human body moving through a still landscape). The only purpose of SEPs is to precisely make possible observing a driven signal that otherwise would be concealed by other concomitant processes.

Relevant to understand our current approach, another EEG study has used task-irrelevant ERPs to examine brain activity that otherwise is not easily observed. (Wolff et al., 2015) have recently published a paper in which they investigated neural activity linked to WM maintenance of visual stimuli that are not actively attended. The problem is that when visual stimuli are no longer attended, for instance during attentional shifts, brain activity regarding memory processes apparently fades even when the stimuli are still being held in memory (Stokes, 2015). In order to reveal this so called activity-silent, they proposed a paradigm that slightly resembles our proposal for investigating body-related cortices during processing of visually perceived information. They used a task-irrelevant visual stimulus that was shown

during the maintenance of the stimuli in memory. These latter stimuli functioned as task-irrelevant impulses to reveal hidden representations of the stimuli to-be-remembered (much alike in echolocation, where simple impulses 'ping' are used to reveal unseen landscapes). Their results showed how a task-irrelevant stimulus may be used to drive a signal that otherwise remains concealed.

We suggest that applying task-irrelevant SEPs while encoding body-related information elicits ERP components arising from body-related cortical regions that otherwise are concealed. Once SEPs are elicited, these act like impulses that reveal processing of body-related information. Importantly, in this context, SEPs *per se* have zero or very little cognitive relevance and their only purpose is to precisely elicit neural impulses that allow subtraction of concomitant components arising from distinctive neural generators.

2.2.4. Considerations in data analysis and inspection

I have introduced the ERP-EEG technique, the distinctiveness of the neural processes during encoding of visually perceived body stimuli, and a new method to isolate their processing beyond the visual stream. In the following sections I revise different methodological aspects that need to be considered in the design and data handling when using this method.

2.2.4.1. Signal to noise ratio

It also important to rule out possible confounds developing from subtractive procedures. For instance, when subtracting activity from visual-only trials (VEPs) from VisualTactile trials' activity (VEPsSEPs) it is important to check that the number of trials in each stimulation condition is similar across other conditions. Otherwise the signal to noise ratio will virtually differ and the ERPs will show interactions and main effects that are not supposed to be there. Comparing the number of accepted trials

across all conditions and testing whether or not these are significantly different is a quick but first effective method of ruling out unwanted surprises.

After checking the number of trials per conditions and computing difference waveforms, it is important to compare source waveforms across cortical regions and conditions. Specifically, somatosensory processing of body-related stimuli is supposed to arise from slightly postcentral cortices regions (i.e., mostly parietal electrode sites) and its activity should be recorded from electrode sites close to this area. If the tactile input is delivered at the very beginning of the trial, it is possible to observe an early component peaking around 45ms after tactile onset, which will likely reflect mere influx of tactile input (Hämäläinen et al., 1990; Eimer and Forster, 2003). Depending on the experimental design, this can be used to estimate from which electrodes it is possible to observe somatosensory processing. In any case, the difference waveform (VEPsSEPs – VEPs) resulting in visually driven SEPs needs to be compared across more anterior and posterior electrode sites. If the procedure has been effective in subtracting components that are present in both stimulation conditions, modulation of waveforms should be only found in expected somatosensory ROIs while waveforms over additional regions should not differ. Precisely, after subtraction it is recommendable to tests these waveforms against zero (no differences), as well as inspecting brain activity from other regions that should exhibit well-known components before subtraction (e.g., inspecting occipital electrode sites after subtraction of VEPs).

2.2.4.2. Accounting for interhemispheric differences

Our own body representation in the brain is lateralised; the right hand is represented over the left sensorimotor cortex and *vice versa.* Similarly, the lateralised dominance in controlling our own body seems to be reflected on the remapping of others' bodies and actions in the our brain (Shmuelof and Zohary, 2006; Goslin et al., 2012). Body-

related stimuli such as images and videos of hand, arm, and leg actions will likely drive brain activity in a lateralized manner (Buccino et al., 2001; Perry and Bentin, 2009). The laterality and point of view of the stimuli conveyed in ERP studies requires considering this element as a unique factor that differs from the hemispace in which information is displayed. For instance, videos showing right hand actions that are displayed from an egocentric point of view on the right side of the screen would probably elicit greater brain responses in the contralateral sensorimotor hemisphere than left hand actions displayed in similar setting. Therefore considering the contralateral representation of body information in the brain, the design and further analysis of waveforms needs to include 'hemisphere' as factor with two levels (i.e., contralateral and ipsilateral).

During inspection of somatosensory processing elicited by SEPs after subtraction of concomitant VEPs, the factor hemisphere can be analysed and ultimately expressed through different linear analysis. The first approach is to conduct a two-way analysis of variance ANOVA after subtraction of VEPS on the mean amplitudes. The resulting SEPs are compared between hemispheres and any other conditions of interest (i.e., Hemisphere (ispi-contralateral) x Condition (body and non-body-related perceptual task). A second approach is to subtract activity between both hemispheres and to compare activity between the remaining conditions by using a t-test. In both cases the p-values will be similar but the type of analysis and the way in which the data is shown in they corresponding figures will differ. Overall, hemisphere should be included as a factor in statistical analyses because body-related stimuli drive lateralized effects. Since interhemispheric differences are regional differences that need to be supported by appropriate tests, if two conditions or groups are different in a region but nor in another one, an interaction of group/condition by region is needed to show this difference (Kappenman and Luck, 2012; Keil et al., 2014). Alternatively,

it is also reasonable to report these effects by showing that one conditions differs from zero (no differences) whereas the second conditions does not.

2.2.5. Considerations about tactile stimulation and its timing in the brain

We proposed the use of SEPs to scrutinise processing of body-related stimuli over body-related cortices. Similar to the effect that differences in visual parameters posses in eliciting different VEPs, there are tactile parameters that need to be taken into account because their possible effects in the later modulations of SEPs. A first important parameter includes the stimulated body part: distal stimulation such as that produced by tactile stimulation on the feet takes generally longer to reach primary somatosensory cortex (S1) compared to stimulation on the hands or face. Secondly, somatosensory stimulation entails different submodalities (i.e., nociception, mechanoreception, thermoreception, proprioception and viscероception). This division follows differences in the afferent routes that go from the body to the brain (Cruccu et al., 2008). In the study of Sel and colleagues (2014), mechanical stimulators elicited information to travel through the dorsal column-lemniscal system. Conversely, the extralemniscal system underpins nocioception in pain studies. Different stimulators elicit diverse pathways towards somatosensory cortices, as well as different sensations, timing, and amplitudes. For instance, electrical stimulation is a relatively uncommon form of stimulation that bypasses sensory receptors. On the other hand, it elicits large SEPs and it is faster than other types of tactile stimulations (Foxe et al., 2000).

Site and type of the stimulation are important factors in the design of experimental paradigms. For instance, if visual stimuli are supposed to be presented in synchrony to stimulation, it is not only relevant to double check the refresh rate of the screen but also how and when tactile stimulation is elicited at a neural level. Lastly, it is important to take into account that because the tactile stimulators produce noise that

could also evoke auditory evoked potentials, white noise should be played during the testing period. This white noise should be equally presented in both ears and should be measured from the participants' head.

2.2.6. Assumptions

The subtractive nature of the method proposed in this article is based on several assumptions. Despite the utility of difference waveforms, the data obtained after subtractions will be always noisier compared to parent waveforms (Luck, 2014). Also, what is actually subtracted needs to be carefully inspected in each individual experiment. For instance, (Teder-Sälejärvi et al., 2002) described how some interactions in multisensory integration could be actually accounted by a double subtraction of an anticipatory ERP that was equally present in all ERPs conditions (i.e., auditory, visual, audiovisual). Therefore, when computing multisensory integration in 'Audiovisual – (Auditory + Visual) waveforms' the anticipatory activity may be subtracted twice, creating the impression of an early interaction due to cross-modal interaction (see a follow up of this issue in Talsma and Woldorff (2005). Parameters such as the participants' expectation and the timing in which the evoked activity is elicited need to be carefully contemplated in subtractive methods.

Another issue concerns the use of different sensory stimulations during encoding of body-related information and its effects on later subtractions. Isolating SEPs by the subtraction 'VEPsSEPs – VEPs' assumes that visual effects are equally distributed across conditions and that once the subtraction is conducted only SEPs modulations would be observed. Nevertheless, the latter could reflect interactions modulated by the integration of sensory input and attentional mechanisms that would specially affect early components (Busse et al., 2005). To avoid this, the physical features of the visual stimuli should be similar in the Visual and VisualTactile conditions (Luck, 2014). If consistency is not feasible (e.g., when comparing body *vs.* non-body-related

stimuli), the stimuli should be well controlled though counterbalancing and the matching of parameters such as timing, size, difficulty, and brightness. Also, it is important to emphasize that the tactile stimulation used to elicit SEPs should be task-irrelevant, so, other unexpected computations are not mistakenly measured.

2.3. Summary

With the advent of new methodologies, the ERP-EEG technique is steadily evolving towards a better temporal and spatial resolution. In this chapter, I considered the essential pros and cons of ERP-EEG technique and framed these in the field of embodiment. A recurrent issue in contemporary ERP research is that the sight of body stimuli elicits visual-evoked activity (VEP) that masks concomitant processes in sensorimotor cortices, known to play a crucial role in processing body-related information. Therefore, it is difficult to tease apart the brain activity in those brain areas from visual carry-over effects. Here we propose a novel method to dissociate visual and body-related cortical processing by the use of visual-evoked potentials (VEPs) and somatosensory-evoked potentials (SEPs). By eliciting SEPs during encoding of visually perceived body stimuli it is possible to probe the state of somatosensory cortex during such process (VEPsSEPs condition). However, the resulting activity contains a mixture activity due to SEPs and VEPs. For this reason it is necessary to include a homologous condition in which the only difference is the absence of SEPs (VEPs-only condition). Then, SEPs are isolated by computing the subtraction of mean average waveforms across conditions (i.e., VEPsSEPs – VEPs). This method allows exploring the involvement of body-related cortices when seeing and encoding bodily-related information with high temporal resolution.

2.4. Artistic Impressions II

Bodily Realm – The method (2015) Photography on board (21 x 29cm) / AGP
This image represents the moment in which a novel method allows to explore the regions that were once occluded in *Artistic Impressions I*. Here the model's hands vanish. *The Method* embodied by the arm, delicately exposes new landscapes to be explored.

2.5 Chapter 2.5: Designing the stimuli to-be-remembered

The experimental work of this PhD thesis is grounded in the three manipulations detailed in *Chapter 2,* briefly*:* (1) the use of stimuli that differ in the type of brain mechanism that they evoke (body *vs*. non body-related visual stimuli), (2) the use of ERP-EEG techniques that evoke brain activity in both visual and body-related sensory cortices (use of somatosensory and visual evoked potentials; SEPs and VEPs), and (3) the design of paradigms that isolate sensorimotor processing by means of subtraction between evoked potentials.

The ERP-EEG technique and the subtraction associated to its analyses have been already described in *Chapter 2.* Here I focus on the first point (i.e., stimuli evoking distinct brain mechanisms), which refers to the use of body and non-body-related stimuli. It is known that body-related stimuli do not only engage those sensory areas participating in the initial sensory acquisition of the information but also additional brain regions that process our own body in the brain (Di Pellegrino et al., 1992; Grezes and Decety, 2001). Since my PhD work seeks to understand how visually perceived body stimuli are maintained in WM, a set of body and non-body-related stimuli (all visual) were created. Including the dissociation of VEPs and SEPs by the use of the aforementioned method, comparing brain activity from participants holding in memory images of body and non-body visual stimuli may allow to ascertain the neural mechanisms underpinning WM for body-related information.

2.5.1 Creating the visual stimuli for studies 1 to 3.

Static images of hands were chosen as stimuli because they should elicit lateralized cortical activity that may arise, in principle, from the lateralized cortical representation

of the hands in the brain (Molenberghs et al., 2012; Perry and Bentin, 2009). This lateralization is crucial for the design and analyses of the studies included in this work (see *Chapter 2* and method sections in further chapters). The neural underpinning of other body parts in the cortex is more centralised and does not provide such well-lateralized activity (Eickhoff et al., 2007). The non-body-related stimuli were polygonal shapes based on the hand images' outlined by using the latter as templates.

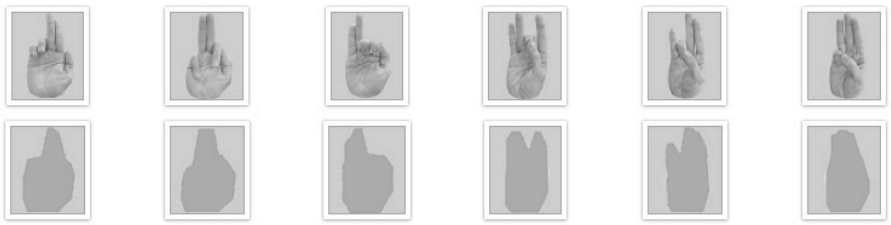
A total of 27 pairs of high-resolution hand images depicting different hand postures and polygonal shapes based on the hands' outline were created. From these visual stimuli, 6 pairs of images were selected. The choice was based on the following criteria: only images that did not convey meaning or symbolism were selected. For instance, a hand posture photographed from the side, depicting a fist with the thumb up could be verbally coded as 'OK'. It was important to avoid semantic coding and elicit brain activity mainly due to bodily or visual coding. Similarly, we wanted to avoid participants counting the number of fingers up (all stimuli have 2 or 3) or using semantics codes (stimuli do not resemble quotidian objects). This set of images was greyscaled, sized, and horizontally mirrored to the left to create 6 more pairs of images depicting left hands and corresponding control stimuli.

Next, two pilot studies including 7 participants each were performed. The aims of these pilot studies were: i) ensuring that behavioural and further electrophysiological markers were correctly synchronized, ii) reducing order effects on the consolidation of the two set of stimuli in memory, iii) and matching difficulty between the control condition (shapes) and experimental condition (hands). This last point is especially important since EEG components are quite sensitive to task difficulty (e.g., Gherri el al., 2015). The procedure of these pilot studies was very similar to the main studies conducted in this thesis. In summary, participants were instructed to recall

differences between pairs of arrays depicting images of hands postures/finger positions or polygonal shapes. In each trial a central arrow cued the participants to covertly attend to the items in either the left or right hemifield. Then, the memory array was presented (100ms) and followed by a blank retention interval (900ms). Next, the test array was displayed until participants verbally response whether the memory and test array were similar or different.

The results from those pilot studies led to the behaviourally matched set of stimuli shown in the Figure 2.5-1. Overall (in the second pilot study, after introducing modifications regarding colour and outline from pilot no.1) participants correctly recalled similarities/dissimilarities in 84% of the trials for both stimulus types in the load 1 condition (holding in memory one stimulus), and 68.5% in load 2 for both stimuli conditions. Furthermore, no order effects were observed (all *ps* > 0.05).

A



B

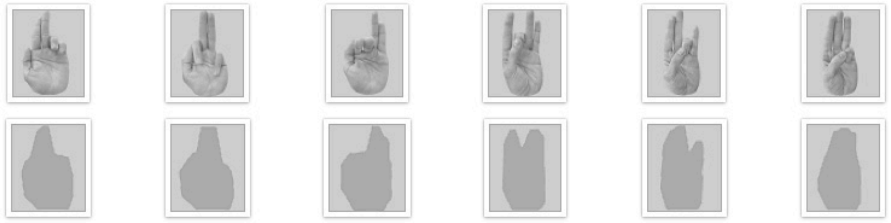


Figure 2-5-1. Final set of body-related and non-body-related stimuli (control). **A**, set of 6 grey scaled right hands depicting hand/finger positions and their equivalent non-body-related stimuli (control conditions). **B**, images of right hands were horizontally mirrored to created stimuli set of left images and correspondent control stimuli.

3. Chapter 3: Neural dissociation for visual and sensorimotor WM: somatosensory brain areas

3.1 Study 1: Introduction

In *Chapter 1* I reviewed prevailing models in the WM field, behavioural evidence for the specific existence of a WM system supporting the encoding of visually perceived body stimuli, and I proposed a number of neural candidates for this latter system. In brief, the neural regions that are likely to underpin WM for body-related stimuli are those contributing to action perception, as well as those underpinning our own cortical representation of the body in the brain, for instance, somatosensory cortices. In *Chapter 2* I revisited the overall ERP-EEG technique and proposed a method that allows isolating somatosensory processing from the simultaneous visual response generated when seeing bodies. In the current chapter, I put into practice this method and investigated whether or not somatosensory cortices play a role in WM for visually perceived body stimuli. To examine this matter, I briefly outline current accounts in WM and I comment on EEG recordings of brain activity linked to WM processing. Secondly, I introduce the hypotheses of the study, its methodological aspects, and results. Third, I discuss the present findings and review the overall limitations.

3.1.1 Sensory recruitment models of WM

Working memory (WM) supports complex behaviours by maintaining task-relevant information (Baddeley, 2003). Persistent activity in perceptual cortices during retention of stimuli in WM has been linked to this process. Such activity is shown in the delayed period, during the consolidation of stimuli in memory, and it seems to be modulated by memory capacity performance specific to the sensory modality in

which stimuli to-be-remembered have been perceived (Vogel and Machizawa, 2004; Katus et al., 2014; McCollough et al., 2007; Katus et al., 2015). The exact properties of this persistent activity and its link to conscious control of attention are still debated. Nevertheless, its occurrence, modulated by memory capacity and load, as well as its sensory foundation have led to state-based models of working memory (D'Esposito and Postle, 2015). These have evolved from those models assuming that WM is underpinned by highly specialised systems (e.g., multicomponent model of WM, Baddeley and Hitch, 1974; Baddeley, 2012). However, the state-based models of WM acknowledge a more dynamic frame where in principle mnemonic content is not strictly supported by a limited number of memory systems; here, WM is more a neural property rather than a specific type of process.

Two approaches arise within state-based models: one considering STM and WM as a reactivated form of LTM and a second approach considering WM as a reestablishment of perceptual experience. The difference between the models is relatively small. Both accounts have originated in the memory literature by studying different types of stimuli (D'Esposito and Postle, 2015). Activated LTM models have been proposed when studying symbolic stimuli such as digits, words, and letters (i.e., semantic content) whereas sensory recruitment models have been articulated when studying the maintenance in memory of colours, gratings, orientations, tactile taps, and auditory tones (i.e., 'more perceptual features'). Nevertheless, both approaches converge upon the encoding of information in WM by activating one of the possible several states of the information. Therefore, a characteristic feature of these accounts is that encoding of information in working memory occurs when activating those internal states of information that are relevant for the on-going task, a process which ultimately leads to stored-featured content that seems to be underpinned by sensory cortices.

3.1.1.1 Sustained activity during visual WM

One of the neural markers associated with WM, the findings of which supported the validity of the sensory recruitment models, is the presence of sustained activity during the delayed period of WM tasks. Specifically, sustained activity refers to that neural activation observed when participants engage in tasks that demand continued attention and mnemonic encoding. The term 'sustained' is often found in the ERP literature while persistent or supra-threshold activity is more present in fMRI studies. Sustained activity was already reported in the seminal work of Fuster and Alexander (1971) and in other important contribution such as the study of Ruchkin (1990).

Remarkably, Vogel and Machizawa (2004) designed a paradigm that elicited sustained activity linked to WM, as well as exploiting the contralateral primary disposition of sensory cortices to isolate such activity from concomitant unspecific (non-memory-related) brain activity. They developed a bilateral change detection paradigm in which participants are asked to hold in memory either items presented in the left or right hemifield while fixating their gaze on a centred cross. Once all perceptual parameters are controlled (e.g., degrees of visual angles from a centred point), the contralateral visual system to the hemifield to-be-remembered exhibits a slow negativity that persists through the whole retention interval of the stimuli in WM. Conversely, the ipsilateral hemisphere exhibits activity closely related to the perception of stimuli that are not to-be-remembered. This manipulation allows for a subtraction of activity from contralateral and ipsilateral hemispheres (i.e., contralateral activity = 'perception + memory encoding and consolidation' minus ipsilateral activity 'perception only') (Fig. 3-1). Therefore this visual component (namely, contralateral delay activity) is supposed to reflect neural activity due to memory-only effects of encoding in experimental manipulations with increasing memory load. To this point the visual contralateral activity (i.e., vCDA) amplitude has

been linked to individual WM capacity (Cowan, 2010; Lefebvre et al., 2013), as well as to filtering capacity (Vogel et al., 2005), and it has been used in experimental paradigms designed to study object tracking, visual search, features binding, and effects of complexity in memory recall (e.g., Drew and Voger, 2008; Carlisle et al., 2011; Peterson et al., 2015; Alvarez and Cavanagh, 2004; respectively).

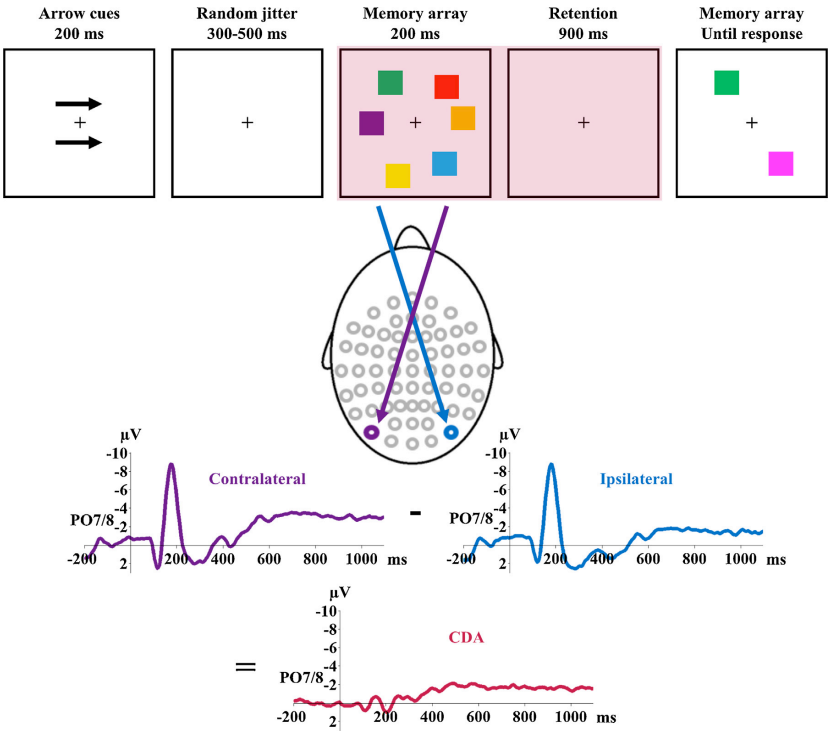


Figure 3-1. An illustration of a typical change detection trial and the resulting CDA waveforms. This example (adapted from Allon et al., 2014) is a grand average of 20 participants, at the PO7/PO8 electrodes, where the CDA is usually most pronounced. Subjects were presented with 3 colors for 200 ms, and had to memorize them during the 900-ms retention interval. The CDA is time-locked to the onset of the memory array, and the activity is measured throughout the retention interval (resulting, in this example, in a 1100-ms long time-window), but before the onset of the test array. Note that the waveforms include both right and left trials, such that the contralateral activity is generated from right electrodes on left trials and left electrodes on right trials (this is an example of a right trial, and hence PO7 registered contralateral activity and PO8 registered ipsilateral activity). The CDA is the subtraction of ipsilateral activity from contralateral activity. *Note*. Reprinted from "The contralateral delay activity as a neural measure of visual working memory" by Luria, R et al., 2016, Neuroscience and Biobehavioural Reviews 2016:62,100-108. Copyright (2016) with permission from Elsevier

3.1.1.2 Sustained activity during tactile WM

As noted in the previous section, several studies have taken advantage of the contralateral organization of visual cortex, describing and isolating visual CDA sensitive to memory capacity (see Luck and Vogel, 2013). Interestingly, not only the visual stream is contralaterally organised; our own cortical representation of the body is also represented in a contralateralised manner. Somatosensory cortices (SCx) offer a similar contralateral organisation, of the body, (left hands represented in right SCx and *vice versa*), underpinning responsiveness (Blakenburg, et al., 2008; Auksztulewicz et al., 2012) and temporary storage of tactile information (Harris et al., 2002; Spitzer et al., 2010; Spitzer and Blankenburg, 2008).

Tactile contralateral delay activity (tCDA) has been described for tactile WM (Katus et al., 2014; Katus et al., 2015), that is, WM for different number of tactile taps, elicited through tactile stimulators, delivered on the participants' body (e.g., fingertips), and registered through EEG. This tCDA follows the same scheme as the vCDA: it is computed by subtracting ipsilateral from contralateral activity and it originates in sensory areas (somatosensory cortices), which are modulated by memory load (number or frequency of tactile taps over the tip of the fingers). Importantly, the tCDA is specific to the hemisphere over the SCx holding the percept in memory. Tactile probes in the form of retro-cues, as well as exchanging the space where tactile stimulation is received when crossing the hands, engage the hemisphere receiving the influx of taps to-be-remembered (Katus et al., 2015).

3.1.1.3 Sustained somatosensory activity linked to visual processing?

Crucially, SCx not only process pure tactile information in a lateralized manner, they are also sensitive to visual bodily information (Shmuelof and Zohary, 2006; Buccino et al., 2001; Keysers et al., 2010). Body-related visual stimuli strongly influence where and how relevant information is processed in the brain (Kanwisher, 2010;

Pitcher et al., 2009; Urgesi et al., 2007), providing additional cortical regions such as SCx tightly linked to an early visual response with functional properties related to human behaviour (Sel et al., 2014; Meyer et al., 2011; Calvo-Merino et al., 2005). Therefore, in addition to visual sensory areas, perception of body images and actions engages our own body representation in sensorimotor and somatosensory cortices (Caspers et al., 2010; Molenberghs et al., 2012). Additional evidence for this comes from a wide range of findings; for instance, several studies have shown that tactile processing of one's body is actually enhanced by seeing others' body sensations (Schaefer et al., 2012; Blakemore et al., 2005). Other studies have shown that observing someone else's pain (Costantini et al., 2008; Martínez-Jauand et al., 2012), as well as observing the mere touch on others' hands may activate the perceiver's somatosensory regions; vicarious tactile processing (Ebisch et al., 2008).

Considering that (1) SCx seems to responds to visual perception of others' bodies, and that (2) sensory recruitment WM models postulate that perceptual regions compute both the percept and its WM maintenance, SCx may allow us to measure sustained activity in form of a visually driven neural signature sensitive to visual memory load (namely visually-driven CDA —vdCDA). This sustained activity could represent a marker of encoding and maintenance of visual body-related information (e.g., hand images) in cortices other than visual.

3.2 Aims, methodological approach, and predictions

Aims of the study. In the current study we sought to answer whether the sensory entry modality or the nature and functional properties of the perceived information dictate where in the brain information is maintained in memory. Specifically, we examined whether or not somatosensory areas (SCx), which participate in processing the body percept, are also involve during active maintenance of the stimuli in memory.

Methodological approach. Items to-be-remembered were hand images and non-body control geometrical shapes (in counterbalanced blocks). By dissociating early visual processing from visually driven but sensory independent cortical activity, we expect to uncover involvement of somatosensory cortices in encoding information during a WM task using body and non-body-related visual stimuli (independent of visual carry-over effects). To this end, we recorded visual-evoked potentials (VEPS) in half of the trials. In the other half, we recorded simultaneous visual and somatosensory evoked potentials (VEPs, SEPs) while participants performed the visual memory task. SEPs were evoked by delivering tactile probes to both index fingers. We subtracted brain activity from visual-only to visual-tactile trials to isolate purely somatosensory responses from carry-over visual effects during this task. Hence, we obtained SEPs free from VEPs in the same WM task. Moreover, based on the lateralisation of the display in the paradigm and the contralateral organisation of visual and somatosensory cortices, we also subtracted ipsilateral from contralateral activity.

The factors of these experiment included: stimulus type (shape, hand images), memory load (1, 2 images), and hemisphere (ipsilateral, contralateral). These factors were computed in the analyses of VEPs and SEPs-after subtraction of VEPs.

Predictions. We predicted that visual-evoked potentials (VEPs) would be modulated by memory load in the non-body-related stimulus condition; this activity would arise from engagement of visual areas over occipital sites (Vogel and Machizawa, 2004; Tsubomi et al., 2013). Additionally, once isolated from visually elicited activity in the same task, SEPs will reveal modulation of brain activity by memory load for body-related stimuli (i.e., increasing number of hand images to-be-remembered) arising from engagement of SCx over parietal electrode sites. With this design and methodology, we sought to identify a new neural signature of a visual memory trace

beyond visual sensory cortices, exhibiting novel evidence for encoding of visual information in functionally different sensory cortical regions that match the perceptual characteristics of the perceived stimuli.

3.3 Methods

participants

Twenty participants (10 males; mean age = 28.5) with normal or corrected-to-normal vision took part and gave informed consent, approved by City University London Psychology Department's Research Ethics Committee. Sample size was chosen based on related studies and paradigms (e.g., Vogel and Machizawa, 2004; Tsubomi et al., 2013; Katus et al., 2014).

Stimuli

A set of 6 pictures of right hands depicting different postures with no meaning or symbolism was used. These hands were mirrored to the left, resulting in 6 pairs of right and left hands that were then greyscaled. For the control condition a set of geometrical shapes was created matching the hands' outline, size, and colour.

Experimental design and procedure

Participants performed a visual memory task (Vogel and Machizawa, 2004) in which items to-be-remembered were hand images (depicting different finger/hand positions) and, in separate blocks, comparable geometrical shapes. Participants were cued on each trial by a central arrow to attend to items displayed in their left or right hemifield. This was followed by a bilateral memory array depicting 1 or 2 items presented in each hemifield (100ms) and then followed by a blank retention interval lasting nearly one second. A final test array that differed in 50% of the cases from the memory array by one item was displayed until participants verbally responded whether or not the memory and test arrays were identical (Fig. 3-2). Participants' forearms rested on the top of a table with their hands separated in palm up position while covered by a

black surface. Visual stimuli were displayed using E-Prime Software (Psychology Software Tools).

All stimulus arrays were presented within two 4.5° x 8.5°rectangular regions that were centred 6° to the left and right of a central fixation cross on a light grey background. Each memory array consisted of 1 or 2 hands (1.3° x 0.8°) in each hemifield. Right hands were shown on the right hemifield while left hands were on the left. Each stimulus was randomly selected from the set of twelve hands. In the control condition 1 or 2 polygonal shapes (1.3° x 0.8°) were selected and shown in a similar fashion. Position of all stimuli was randomized on each trial with the constraint that the distance between stimuli within a hemifield was at least 2.4° (centre to centre).

Visual-tactile trials. In the other 50% of the trials, we elicited simultaneously VEPs and SEPs by applying task irrelevant single tactile taps simultaneously delivered to both hands on the tip of the participants' index fingers at the onset of the visual memory array. Tactile stimulation was applied using two 12 V solenoids driving a metal rod with a blunt conical tip that contacted with participants' skin when a current passed through the solenoids. Both solenoids were placed on the tip of the index fingers, one for each hand. To mask sounds made by the tactile stimulators, white noise (65 dB, measured from participants' head) was presented through a loudspeaker centrally positioned 90cm in front of the participants.

This mechanical stimulation allowed us to probe the state of the SCx, exposing its underlying processing during memory encoding and maintenance of the visual stimuli by measuring the electrocortical activity (SEPs) elicited by task irrelevant tactile taps. To be able to isolate somatosensory processing (over and above carry over visual effects) over corresponding parietal electrode sites, we subtracted brain activity from those trials containing activity only due to VEPs (*visual-only* trials) to those trials containing a combination of visual and somatosensory activity due to the combined

VEPs-SEPs (*visual-tactile* trials). This allows isolating and observing somatosensory processing free of visual evoked activity (SEPs, VEPs-free) (Sel et al., 2014).

Tessari and Rumiati (2004) showed that a mixed presentation of stimuli belonging to different categories is likely to involve intermixed, multiple, and overlapping encoding memory routes. Conversely, they showed that blocked designs allow observing a more clear involvement of discrete memory mechanisms. Since we sought to examine the specific involvement of SCx during encoding of hands and shapes stimuli (i.e., non body and body-related categories), the composition of the experimental list in the present study was blocked rather than mixed by stimulus condition. Specifically, We counterbalanced participants across stimuli conditions. Half of the participants started the experiment with the hand stimulus condition; performing 672 trials across 8 blocks with breaks every 84 trials. Then, they completed similar number of trials, blocks, and breaks in the shape stimulus condition. In each trial the number and stimulus to-be-remembered were randomly selected from the corresponding stimulus set (i.e., specific hand postures or shape outlines). Similarly, the task-irrelevant tactile taps were randomly applied across half of the trials at the onset of the memory array. Overall, participants performed a total of 1344 trials, 672 for each stimulus condition (hands and geometrical shapes). This is equal to 336 trials for each load condition (load 1 and 2) of which half entailed the presentation of a task irrelevant tactile probe stimulus (visual-tactile trials) and the other half were visual only trials (visual-only trials).

Participants' sensitivity to detect changes.

As indicated before, the test and memory arrays different in 50% of the cases by one item and participants verbally responded whether or not these were similar or different. Specifically, participants responded *'yes'* and *'no'* to indicate 'same' and 'different' , respectively. Afterwards, these responses were converted to proportions

of hit rates and false alarms that were used to calculate the index of sensitivity *d',* which in theory considers individuals as active perceivers in conditions of more or less uncertainty. This index measures the distance between signal and noise means in standard deviation units. A value of 0 denotes that participants do not distinguish signal from noise, in other words, the do not detect differences between the old stimuli presented in the memory array and the new/different stimuli presented in the test array. Conversely, higher values of *d'* indicate increasing capacity to distinguish the corresponding stimuli. In the context of the current experiments the proportion of 'same trials' in which participants were right and the proportions of different trials in which participants were wrong were calculated. Then, these hit rate and false alarm proportions were subjected to the inverse of the normal cumulative distribution that is specified by the mean and standard deviation ($d' = Z(H) - Z(F)$).

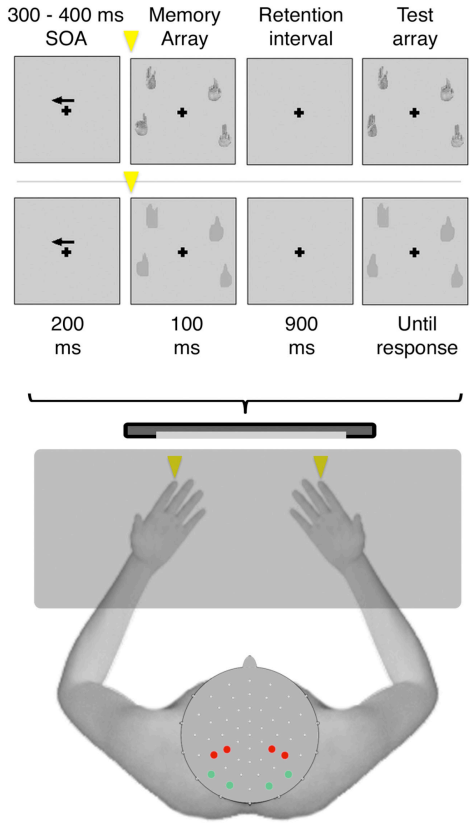


Figure 3-2. Task design and procedure study 1. Participants performed both conditions in counterbalanced order. On 50% of the trials, task irrelevant tactile stimulation was applied to both index fingertips at the onset of the memory array (yellow triangles). Participants verbally responded whether the memory array and test array were the same or different. Electrode map showing electrodes over somatosensory (red) and visual (green) areas included in the statistical analyses. SOA: stimulus onset asynchrony.

EEG recording and data analysis

Both conditions were performed in an electromagnetically shielded room using a 75Hz LCD monitor. Event-related potentials were recorded with active electrodes from 64 scalp electrodes mounted equidistantly on an elastic electrode cap (M10 montage; EasyCap). Electrodes were referenced to the right earlobe and re-referenced to the average reference off-line. Vertical and bipolar horizontal electrooculogram was recorded for eye movements tracking and artifact correction purposes. Continuous EEG was recorded using a BrainAmp amplifier (BrainProducts; 500 Hz sampling rate). Off-line EEG analysis was performed using Vision Analyzer software (BrainProducts). The data were digitally low-pass-filtered at 30 Hz, and ocular correction was performed (Gratton et al., 1983). The EEG signal was epoched into 1300ms segments, starting 200ms before the sample arrays of each trial. Segments were then baseline corrected to the first 100ms, and artifact rejection was computed eliminating epochs with amplitudes exceeding ± 85 μV.

Grand averages were computed independently for hand and shape stimuli conditions, separately for the two memory loads and for visual and visual-tactile trials by averaging brain waveforms elicited at electrodes over the hemisphere contralateral and ipsilateral to the items to-be-memorized as indicated by the central cue. Visual contralateral delay activity (vCDA) was calculated as the difference between mean amplitudes recorded at right hemisphere electrode sites when participants were cued to the left side of the memory array and vice versa, removing thus any contribution of nonspecific bilateral neuronal activity, and separately calculated for load 1 and load 2 for the shape and hand conditions in the 300-900ms time window after onset of the sample array. Statistical analysis was performed for mean amplitudes at occipital and posterior parietal electrode sites (O1, O2, midway between PO7/P7, and midway PO8/P8 of the 10-20 system) (Vogel and Machizawa,

2004; Vogel et al., 2005; McCollough et al., 2007). In addition, we also analysed the effect of time course in 9 consecutive time windows of 100ms from the onset of the visual stimuli (Tsubomi et al., 2013). Mean amplitudes were compared across conditions by analysis of variance (ANOVA).

We computed contralateral waveforms of somatosensory processing from trials in the visual-tactile condition. Visually driven contralateral delay activity (vdCDA) was calculated as the difference between mean amplitudes recorded at right hemisphere electrode sites when participants were cued to the left side of the memory array and vice versa. The underlying activity of somatosensory cortices when maintaining in memory visually acquired stimuli was analysed over parietal electrode sites at CP3/CP4 and CP5/CP6 of the 10-20 system. Then, to isolate somatosensory processing from the visual activity elicited by the onset of the stimuli on the screen, we removed VEPs by subtracting mean voltage amplitude of grand averaged VEPs on visual-only trials from the mean amplitudes of grand averaged ERPs on visual-tactile trials (containing both somatosensory evoked potentials; SEPs and VEPs) (Sel et al. 2014). This subtractive methodology based on evoked activity from different neural sources has been commonly used to study multiple sensory modalities (Talsma et al., 2010; Senkowski et al., 2007; Talsma and Woldorff, 2005). In our specific case, to test SCx encoding of hands driven by the onset of the visual array, synchronously to VEPs, SEPs elicited by task-irrelevant tactile stimulation were employed (Sel et al. 2014). Under such conditions, evoked activity would contain a contribution from both sensory cortices elicited by VEPs and SEPs. This leads to the use of an only VEPs condition, which allows i) the examination of brain activity of visual cortices, ii) the subtraction of visual carry over effects over somatosensory cortices, and the consequent analysis on iii) effects of memory load over both

cortices. When appropriate, Greenhouse-Geisser adjustments to the degrees of freedom were applied, and *p* values were corrected using Bonferroni correction.

Estimating neural generators of the visually driven signal (e-LORETA, CSD)

We used several approaches to estimate the neural generators of the EEG components in the experimental condition leading to a modulation by memory load (i.e., hand condition). We initially used eLORETA, BESA, and Current source density (CSD). Despite computing the forward-search dipole localization algorithm Brain Electric Source Analysis (BESA; Scherg and Berg, 1991), we did not embrace this approach because the forward model requires applying a number of localizers that need to be manually generated based on previous research and data assumptions need to be made. Given the novelty of our paradigm, we avoided this step. On the other hand, we did actually include the data from eLORETA and CSD. However, caution needs to be taken when considering the former model. Even when the estimated brain areas generating the visually driven signal (vdCDA) seem to correspond to those cortices eliciting the SEPs (VEP free), the CDA/vdCDA involves subtraction and computing a virtual signal that represents a single hemisphere modulated by memory load. However, eLORETA and sLORETA estimate neural generators/source localization based on spreading of brain activity in both hemispheres.

Exact low resolution brain electromagnetic tomography

Based on the scalp-recorded electric potential distribution, the exact low resolution brain electromagnetic tomography (eLORETA) (Pascual-Marqui, Michel and Lehmann, 1994; Pascual-Marqui, 2002; Pascual-Marqui, 2007) was used to compute the cortical three-dimensional distribution of current density associated to somatosensory-evoked activity (SEPs). The eLORETA method is a discrete, three-dimensional distributed, linear, weighted minimum norm inverse solution, and it has

no localization bias even in the presence of structured noise. The particular weights used in eLORETA endow the tomography with the property of exact localization to test point sources, yielding images of current density with exact localization, albeit with low spatial resolution (i.e. neighboring neuronal sources will be highly correlated). In the current implementation of eLORETA, computations were made using the MNI152 template with the three-dimensional solution space restricted to cortical gray matter, as determined by the probabilistic Talairach atlas and anatomical labels as Brodmann areas are also reported using MNI space, with correction to Talairach space (Lancaster et al., 2000; Mazziotta et al., 2001; Brett, Johnsrude and Owen, 2002). Source estimation was performed on those time windows where analyses showed significant differences by memory load (i.e., differential activity of candidate brain regions when holding in memory different number of hand postures). This was done after subtracting VEPs and ipsilateral from contralateral activity, specifically, in the time windows from 200-300 ms, and 300-900ms. We constructed whole brain topographical maps by mirroring vdCDA to both hemisphere, then, eLORETA was estimated.

Current source density analysis (CSD).

In addition to eLORETA, we estimated the neuronal generator patterns contributing to our results by transforming the scalp-recorded EEG to surface Laplacians. Such transformation leads to a conservative estimate of the neuronal generator patterns underlying the EEG signal (Nunez and Westdorp, 1994; Tenke and Kayser, 2012; Perrin et al., 1989), in which regardless of the orientation, location, number, or extent of active neural tissue, the effects of volume conduction from distant sources is reduced and a reference-independent representation of EEG/ERP data is obtained. Here, voltage levels (μV) at electrodes by valid head coordinates were transformed through CSD (units in $\mu V/m^{2)}$. This was obtained by transforming scalp potentials

resulting from voltage distribution on the surface of the head at a fixed time to surface Laplacians (lambda: 10^{-5}, order of splines *m*: 4, legendre polynomial: 10) (Katus et al., 2014; Nunez and Westdorp, 1994). As voltage distribution is known at the electrodes, the procedure of spherical spline interpolation was used to compute the total voltage distribution.

The CSD topographical maps of the visually driven CDA (vdCDA, VEP-free) were calculated as the earlier scalp-recorded EEG data by calculating the difference between contralateral and ipsilateral mean amplitudes, and separately calculated for load 1 and load 2 for the hand condition in the 200-300 and 300-900ms time windows after onset of the sample array. Statistical analysis was performed by analysis of variance and included mean averages of electrode sites along the scalp from anterior to posterior regions, respectively of the 10-20 system: midway between F7/AF7 - F8/AF8, and AF3/AF4; F5/F6 and F1/F2; FC5/FC6 and FC3/FC4; C5/C5 and C3/C4; CP3/CP4 and CP5/CP6; midway between PO3/P5 - PO4/P6, and P1/P2; midway between PO7/P7 - PO8/P8, and O1/O2. When appropriate, Greenhouse-Geisser adjustments to the degrees of freedom were applied, and *p* values were corrected using Bonferroni correction.

3.4 Results

3.1.1 *Behavioural data*

Given the nature of our ERP subtraction methodology, it is possible that differences in the signal-to-noise ratio in different conditions could bias our results. To rule out this possibility, we additionally examined the number of accepted trials separately for trials cued to the left and right hemifield, for each memory load and type of stimuli in the *visual-tactile* and *visual-only* conditions. The results showed no effects of cue ($F_{(1,19)} = 1.017$, $P = 0.326$), tactile stimulation ($F_{(1,19)} = 0.727$, $P = 0.404$), stimulus type

($F_{(1,19)}$ = 0.000, P = 0.997), nor a interaction between the previous the factors ($F_{(1,19)}$ = 0.122, P = 0.731). These analyses imply that signal-to-noise ratio did not bias the results on later subtractions across conditions. These analyses imply that signal-to-noise ratio did not bias the results on later subtractions across conditions. Therefore, any dissimilarity on mean voltage amplitude showed on parietal electrode sites was due to the increasing number of hand images to be held in memory.

Participants correctly reported differences or similarities between the memory and test array in 77.3% of all trials in the visual-only condition and in 77.4% of all trials in the visual-tactile condition. Their performance was analysed using the sensitivity index *d'*, which considers false alarms and hit rates, representing then a more precise measurement of signal detection than accuracy only. Repeated-measures ANOVA showed neither an interaction between condition (visual-only and visual-tactile), memory load, and types of stimuli ($F_{(1,19)}$ = 1.076, p = 0.313) nor a main effect of stimulus type ($F_{(1,19)}$ = .022, p = 0.883), nor main effect of condition ($F_{(1,19)}$ = .078, p = 0.782). Lastly, when comparing individually each single condition in the visual-only condition to its equivalent visual-tactile condition, no significant differences were found (all *ps* > 0.108*).* Overall, performance in the hand and shape conditions was very similar, and this similarity was found regardless of whether the trial included tactile stimulation as a single task-irrelevant tactile tap at the onset of the stimuli to be remembered or not (Fig. 3-3).

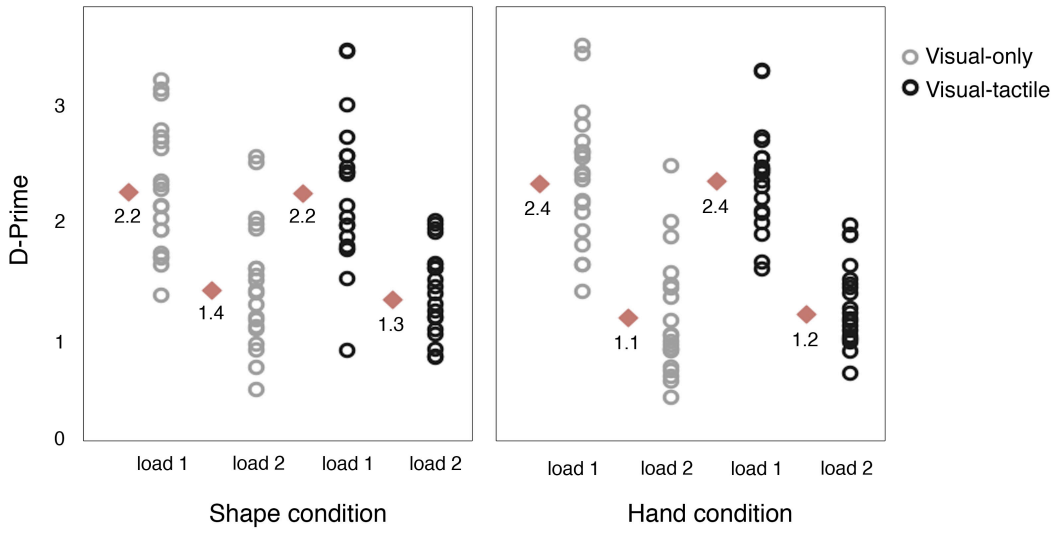


Figure 3-3. Behavioural results in all conditions study 1. Dots represent the means of individual participants, the red diamond the sample average. Overall performance in hand and shape conditions was similar and no significant differences were found between performance for memory load 1 and 2 in the hand and shape conditions regardless the tactile probes (*all ps* ≥ 0.05), *n*=20. D-prime: sensitivity index, d' = Z (hit rate) – Z (false alarm rate).

3.1.2 Visual evoked potentials

This section includes those analyses concerning the visual contralateral delay activity (vCDA) on visual-only trials. Here, VEPs elicited at occipital electrode sites contralateral and ipsilateral to the memorized hemifield were analysed for the different memory loads and stimuli. A sustained negativity appeared circa 300ms after the onset of the sample array over visual cortex contralateral to the memorized hemifield. This visual contralateral delay activity lasted for the entire retention interval and increased with the number of items to be stored in working memory (Fig. 3-4).

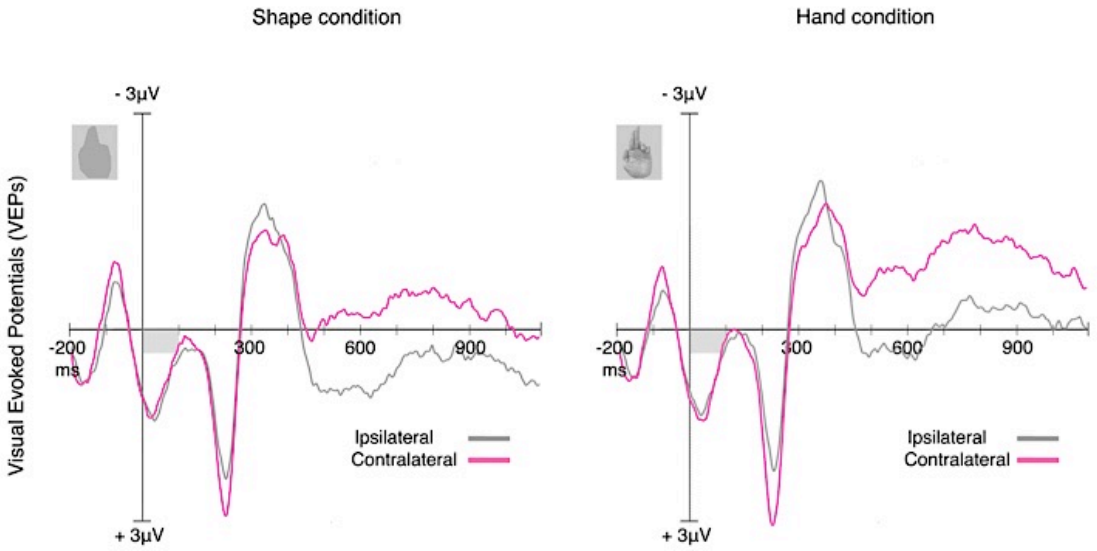


Figure. 3-4. Ipsilateral and contralateral waveforms in shape and hand stimuli conditions. Visual-evoked potentials (VEPs) ipsilateral and contralateral to the cued side of the memory array pooled over lateral occipital and posterior parietal electrodes (midway between PO7/P7 - PO8/P8, and O1/O2 of the 10-20 system). Grey bars indicate the memory array duration.

We inspected this modulation of activity across memory loads by subtracting brain waveforms from ipsilateral to contralateral activity for each array size, removing thus any contribution of nonspecific bilateral neuronal activity. We then computed a repeated-measures ANOVA for each stimulus condition with hemisphere (contralateral and ipsilateral) and memory load (1 and 2) as factors. In the shape condition, the interaction hemisphere by load yielded a significant main effect of mean amplitudes of load ($F_{(1,19)} = 14.106$, $p = 0.001$), hemisphere ($F_{(1,19)} = 11.679$, $p = 0.003$), as well as a significant interaction between load and hemisphere ($F_{(1,19)} = 8.929$, $p = 0.008$). Then, we performed follow-up t-tests comparing brain activity from ipsilateral and contralateral hemispheres in each memory load condition. We found significant differences between ipsilateral and contralateral hemispheres' mean amplitudes in load 2 ($t_{(19)} = 4.407$, $p < 0.001$). Interestingly, vCDA was also observed in the hand image condition and we found significant main effects of load ($F_{(1,19)} = 11.638$, $p = 0.003$) and hemisphere ($F_{(1,19)} = 19.090$, $p < 0.001$). However, repeated-

measures ANOVA in the hand stimulus condition yielded no significant interaction between the hemisphere and memory load factors ($F_{(1,19)} = 0.184$, $p = 0.673$) (Fig. 3-5). These results suggest that hand stimuli are also visually processed in this visual WM task. However, the evoked neural response did not elicit an interhemispheric difference modulated by load, which is indeed the characterizing feature of the vCDA (Luck and Vogel 2013).

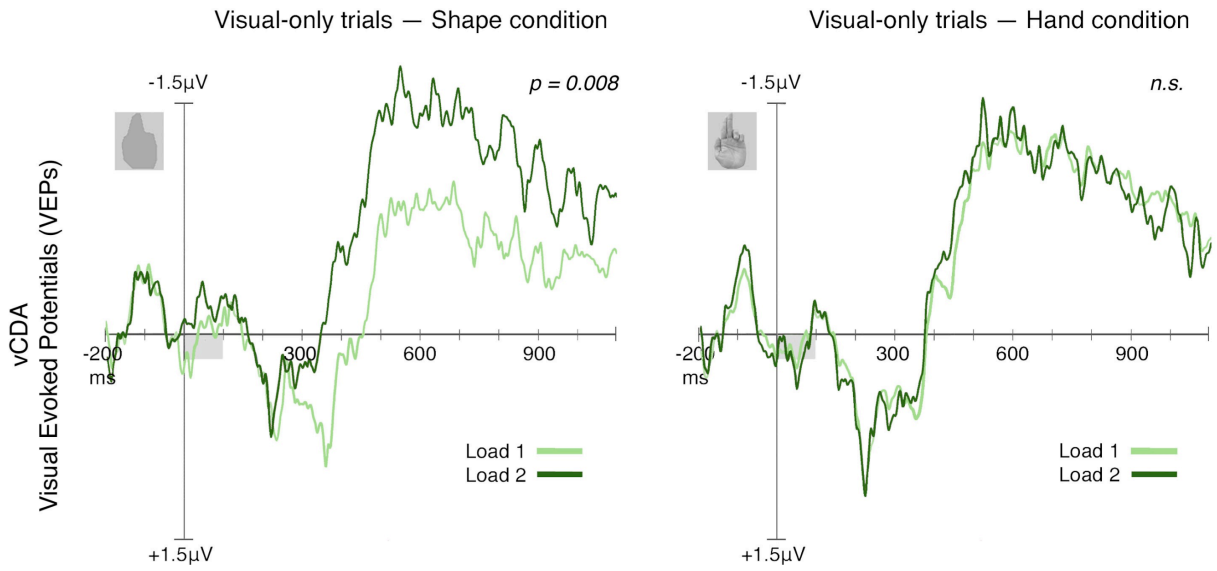


Figure 3-5. vCDA - Visual-evoked potentials (VEPs). Visual contralateral delay activity (vCDA). Contralateral minus ipsilateral visual-evoked potentials (VEPs) pooled over lateral occipital and posterior parietal electrodes for each memory load and stimulus conditions separately. Analysis of variance yielded a significant difference between memory load 1 and 2 in the shape control stimulus condition ($p = 0.008$). No difference was found in the hand image stimulus condition ($p = 0.673$).

3.1.3 Somatosensory VEP-free Evoked potentials

This section includes those analyses concerning the visually driven contralateral delay activity (vdCDA) on visual-tactile trials**.** To observe the pattern of neural responses within SCx in the visual memory task, over and above the carryover effects induced by visual activations elicited in the same task by the onset of the visual displays, we subtracted the mean amplitude of purely visually evoked activity

(visual-only trials) from the mean amplitude containing both visual and tactually probed somatosensory activity during the same memory task (visual-tactile trials) (Fig. 3-6). If SCx activity during memory storage of visually depicted body information reflects a truly somatosensory response, then tactually evoked responses should be differentially affected by the number of hand images (memory load) to be held in visual working memory.

We analysed SEPs after subtractions of VEPs for both memory loads and stimuli types. Specifically, a repeated measures ANOVA with hemisphere (contralateral, ipsilateral), memory load (1,2), and stimulus factors (hand, shapes) yielded a significant triple interaction between all factors ($F_{(1,19)} = 10.447$, $p = 0.004$). We followed up the latter interaction by the stimulus factor. In the geometrical shape stimulus condition we did not find any significant effect of hemisphere ($F_{(1,19)} = 0.053$, $p = 0.820$), load ($F_{(1,19)} = 0.001$, $p = 0.975$), nor interaction between these two factors ($F_{(1,19)} = 1.210$, $p = 0.285$). In the hand condition, we found no main effects of hemisphere ($F_{(1,19)} = 2.512$, $p = 0.130$) and load ($F_{(1,19)} = 0.178$, $p = 0.678$). However, we found a large negative-going voltage modulated by memory load from 300 to 900ms over the somatosensory cortex contralateral to the visually cued hemifield. This interhemispheric difference showed significantly larger amplitudes as the number of items to be remembered increased (i.e., hemisphere x load interaction) ($F_{(1,19)} = 11.846$, $p = 0.003$). We performed follow-up t-tests comparing mean amplitudes from ipsilateral and contralateral hemispheres for each memory load. We found a significant difference between ipsilateral and contralateral hemispheres' brain activity in the memory load 2 condition ($t_{(19)} = 2.775$, $p < 0.012$). This *visually driven* CDA revealed in SEPs (VEP-free) was only present in the hand condition and over parietal electrode sites (Fig. 3-7 and Fig. 3-9). No significant interaction between hemisphere and load was found when memorizing geometrical shapes.

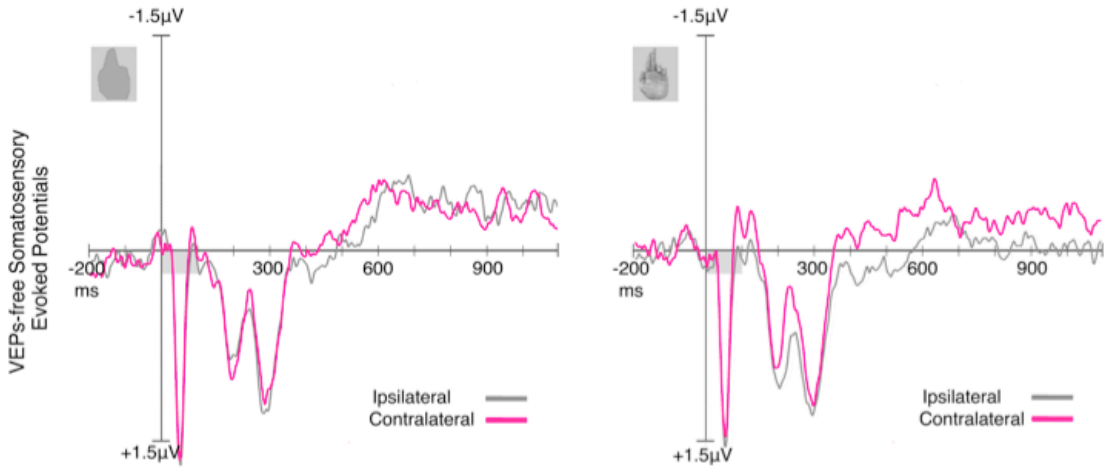


Figure 3-6. Visual-tactile minus visual-only waveforms. Somatosensory-evoked potentials (SEPs) ipsilateral and contralateral to the cued side of the memory array pooled over lateral parietal electrodes (CP3/CP4 and CP5/CP6 electrodes of the 10-20 system), after subtracting carryover visual effects from the visual evoked responses (SEPs VEPs-free). Grey bars indicate the memory array duration.

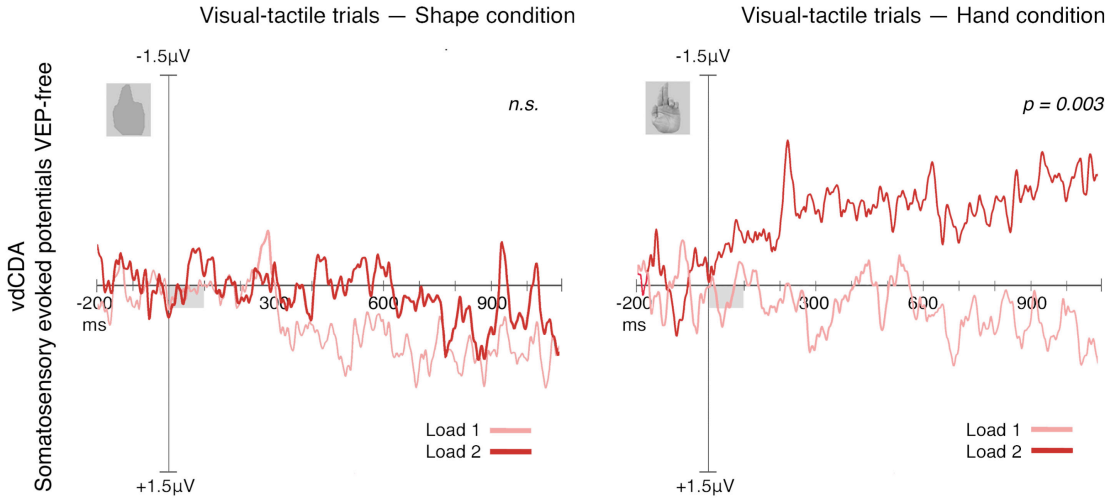
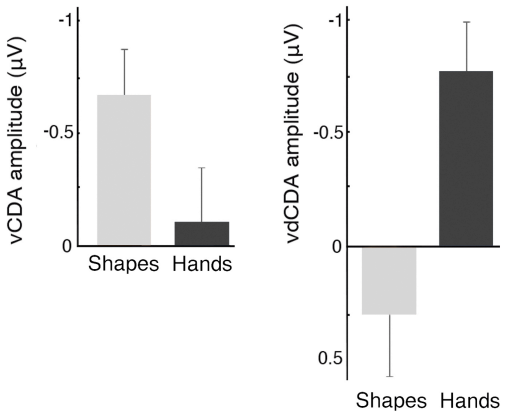


Figure 3-7. vdCDA - Somatosensory evoked-potentials SEPs (VEPs free). Visually driven contralateral delay activity (vdCDA) from SEPs (VEPs free). Contralateral minus ipsilateral somatosensory-evoked potentials (SEPs) pooled over lateral parietal electrodes for each memory load and stimulus conditions separately after subtracting carry over visual effects from VEPs contained in the visual-tactile condition. Analysis of variance yielded significant Hemisphere x Load x Stimuli interaction (P = 0.004), driven by a significant difference between memory loads in the hand image condition ($P = 0.003$). No differences were found in the shape condition ($p = 0.285$); left panel. Grey bars indicate the memory array duration; ns, non-significant; n=20.

Figure 3-8. vCDA and vdCDA amplitude differences. Activity from ipsilateral electrode sites subtracted from contralateral sites in load 1 minus load 2 for both stimuli conditions. Error bars represent within subject SEMs.



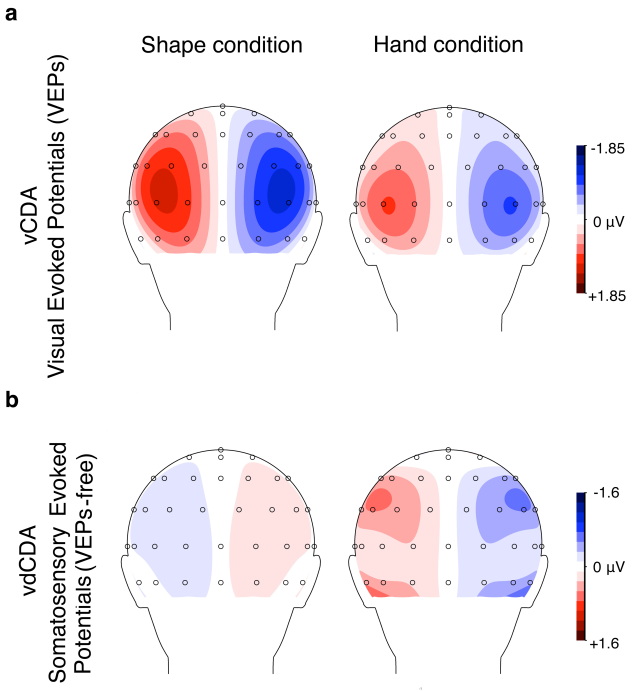


Figure 3-9. Topographical maps of the visual contralateral delay activity (vCDA) and visually driven contralateral delay activity (vdCDA). ***A****,* topography of the vCDA elicited by visual-evoked potentials (VEPs) in shape and hand stimulus conditions 300-900ms after onset of the memory array in load 2, showing an occipital-parietal peak, prominent in the shape condition. ***B****,* topography of the vdCDA elicited by somatosensory-evoked potentials (SEPs) from which brain activity due to visual processing was subtracted 300-900ms after onset of the memory array in load 2, showing a lateral parietal peak, only in the hand condition. Topographic maps were derived by subtracting activity at electrodes ipsilateral from contralateral to the cued side and then from electrodes over the right minus left hemisphere. This activity was then mirrored to the opposite hemisphere to generate whole head topographic maps.

We also investigated the time course of the vdCDA by analysing consecutive 100 ms time windows (Tsubomi et al. 2013). Specifically, we analysed differences of mean amplitudes in the hand stimulus condition across bins of 100 ms between 300-900ms modulated by hemisphere and memory load (i.e., time window x hemisphere x load). No discernible differences were found along the binned waveforms during the retention interval (300-900 ms) ($p > 0.05$), suggesting a steady sustained activity during the retention interval. Interestingly, we also explored the neural response that preceded the 300-900 ms contralateral sustained negativity (Fig. 3-10). We found a significant main effect of hemisphere ($F_{(1,19)} = 5.607$, $p = 0.029$) and a significant interaction of hemisphere by load. This was revealed as significant interhemispheric difference sensitive to memory load in the SEPs (VEPs-free) between 200 and 300 ms of the stimuli onset ($F_{(1,19)} = 16.057$, $p = 0.001$) (0-100 and 100-200 ms bins yielded non-significant results). Here, the follow-up t-tests showed a significant difference between ipsilateral and contralateral hemispheres' mean amplitudes in load 2 ($t_{(19)} = 3.799$, $p < 0.001$).

We named this component *visually driven N2cc* (vdN2cc), which resembles previously described contralateral negativity to the attended hemispace in visual and tactile working memory and attention tasks (N2pc and N2cc, respectively) (Eimer 1996; Eimer and Grubert 2014; Katus et al. 2015a). In particular these components have been associated with attentional selection preceding encoding of information in working memory. This suggests that also the topography and neural generators of attentional selection mechanisms depend on the functional properties of the perceived stimulus (i.e. somatosensory cortex for the attentional selection of body images).

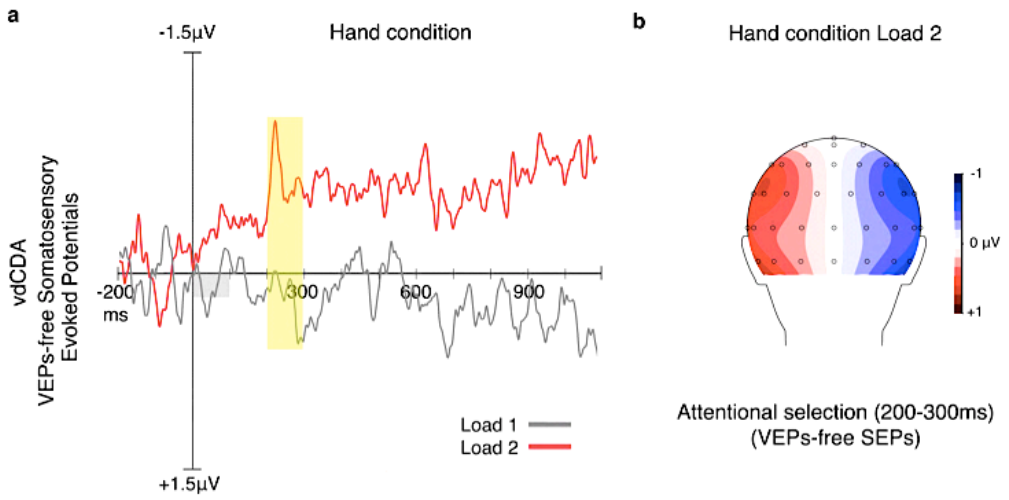


Figure 3-10. Attentional component: Visually driven N2cc (vdN2cc). ***A,*** differences waveforms of contralateral minus ipsilateral VEP-free SEPs pooled over lateral parietal electrodes (CP3/CP4 and CP5/CP6 electrodes of the 10-20 system) for each memory load (visual processing subtracted). The red line indicates the analysis window (200-300ms) for which analysis of variance yielded significant difference between memory load 1 and 2 in the hand posture condition only (P = 0.001), n=20. This period was also used to plot the topographical map in the right, which precedes the time window of the vCDA and vdCDA (300-900ms). ***B,*** topographic map for lateralized brain activity in the 200 to 300 ms analysis window for memory load 2 in the hand posture condition confirmed a lateral parietal activity peak. The topographic map was derived by subtracting activity at electrodes ipsilateral from contralateral to the cued direction and then from electrodes over the right minus left hemisphere. This activity was then mirrored to the opposite hemisphere to generate a whole head topographic map.

3.1.4 Source localization

Exact Low-Resolution Brain Electromagnetic Tomography (eLORETA)

Based on the scalp-recorded electric potential distribution, exact low-resolution brain electromagnetic tomography (eLORETA) (Pascual-Marqui, 2007) was used to estimate cortical source estimation. This was performed on the visually driven activity for the hand postures condition (200-300 ms; 300-900 ms), conditions in which memory load significantly modulated the mean amplitude of SEPs (VEP-free), by identifying a set of regions whose peak of activity was maximal when holding in

memory two hands depicting different postures compared to a single hand posture. In the 200-300 ms time windows, maximal differential activity was source localized in primary somatosensory cortices Brodmann areas (BA) 1/2/3, secondary BA40, and associative BA5. For the 300-900 ms time windows, maximal differential activity between memory loads was localized in these same areas BA 1/2/3 and B40 (Fig. 3-11). Importantly, sensory input, and latter attentional and mnemonic activity (200-300 ms, 300-900ms) are localized in similar somatosensory regions, suggesting functional processing in terms of stimuli representation, neural source, and function.

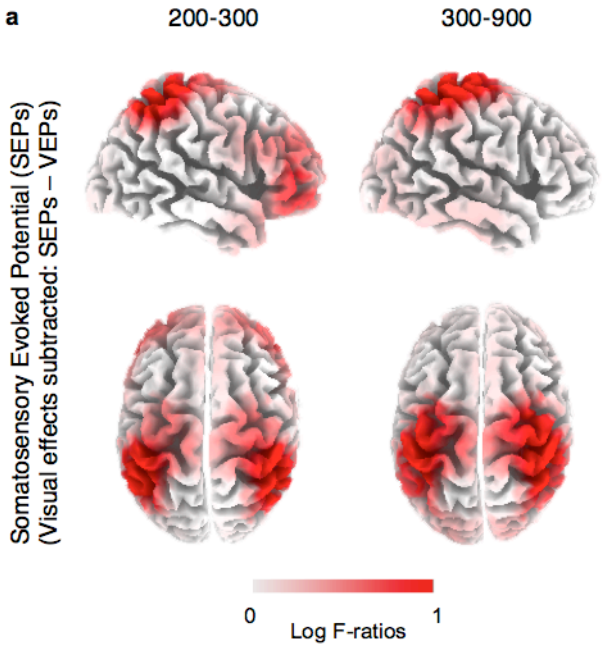


Figure 3-11. Candidate brain areas in vdn2cc and vdCDA. Source localization maps generated by eLORETA. vdN2CC and vdCDA components corresponding to the 200-300ms and 300-900ms time windows of the hand stimulus condition (SEPs, VEPs-free). The areas in red show a lateral parietal activity peak, which corresponds to those areas exhibiting a modulation by memory load. The topographic map was derived by subtracting activity at electrodes ipsilateral from contralateral to the cued direction and then from electrodes over the right minus left hemisphere. This activity was then mirrored to the opposite hemisphere to generate a whole head topographic map.

Free reference estimation of neural generators: current source density (CSD)

Current source density (CSD) analysis was conducted to examine the underlying sensory specificity of the vdN2cc and vdCDA and to validate the correct selection of lateral-parietal electrode sites. For this purpose, we converted scalp potentials to surface Laplacians. Irrespective of the orientation, location, quantity, or extension of active neural tissue, such conversion reduces the effects of volume conduction from distant sources and offers a reference-independent representation of EEG/ERP data. CSD topography offers a conservative estimate of the neuronal generator patterns contributing to scalp-recorded EEG (Nunez and Westdorp, 1994; Tenke and Kayser, 2012; Perrin et al., 1989). Then, we newly isolated the sensory response elicited by the tactile probe in VEP-free SEPs. Here, we checked and confirmed the presence of the P50 component over central-posterior electrode sites circa 50 ms after applying tactile taps (Fig.3-12A), a sensory response shown to reflect influx of tactile input into primary SCx (Hämäläinen et al., 1990; Eimer and Forster, 2003). Next, we proceed to examine the later development of the CSD signal from SEPs VEP-free by computing the difference between contralateral and ipsilateral brain activity for the different memory loads in the hand condition.

We found a well-defined negativity over parietal regions, which increased with the number of hand images to be remembered in the time window of the vdN2cc ($F_{(1,19)}$ = 9.958, p = 0.005) and vdCDA ($F_{(1,19)}$ = 12.001, p = 0.003) (Fig. 3-12). In both components no significant differences were found over more frontal and posterior electrode sites (all ps > 0.130). Interestingly, a slightly anterior to posterior shift can be observed over time in the CSD topographies. This is likely to reflect the underlying mechanism involved in processing visually acquired bodily information; a process known to elicit activity over posterior parietal brain regions such as secondary somatosensory and associative cortices in studies of action and touch observation,

where visuomotor transformation, somatosensory spatial discrimination, and integration of proprioceptive signals seem to play a crucial role (Meyer et al., 2011; Kuehn et al., 2014; Ebisch et al., 2008; Schaefer et al., 2009).

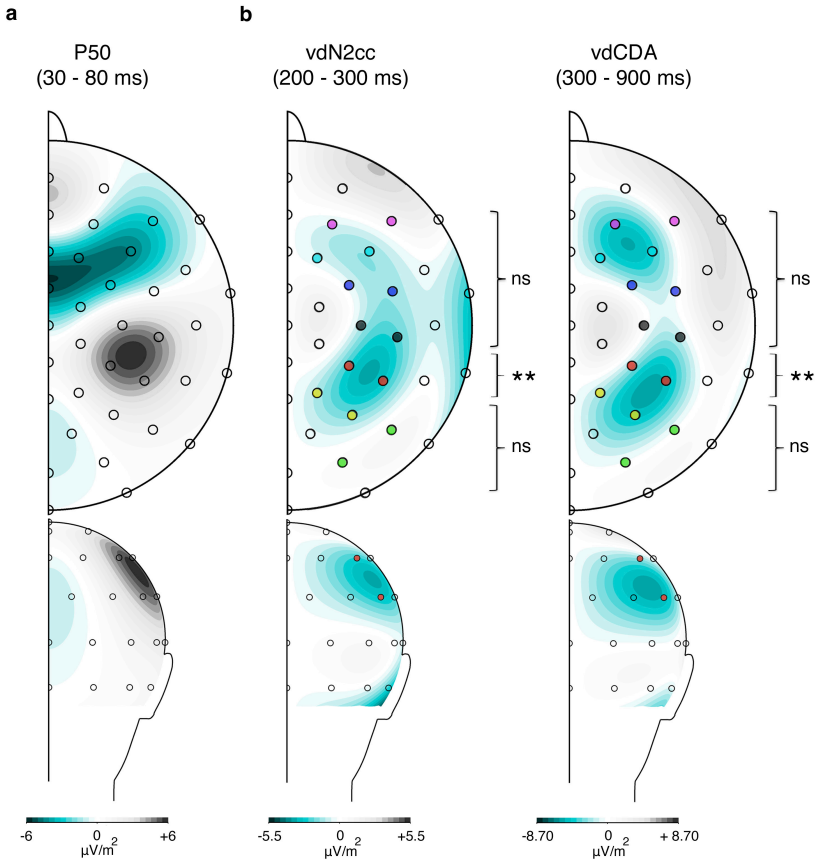


Figure 3-12. CSD topographical maps SEPS (VEP-free) in the hand images condition. ***A,*** CSD scalp distribution in the P50 time windows after collapsing contralateral and ipsilateral evoked potentials for both memory loads revealed an early positivity over central-parietal electrodes upon arrival of brief tactile probes. ***B,*** CSD scalp distribution in the vdN2cc and vdCDA time windows of somatosensory-evoked potentials in the memory load 2 minus load 1 condition after subtracting ipsilateral from contralateral activity. Analysis of variance yielded significant difference between memory loads over the parietal electrode sites (CP3/CP4 and CP5/CP6 electrodes of the 10-20 system -in red). No significant differences were found over more anterior and posterior scalp regions. **, $p < 0.01$; ns, non-significant, n=20.

3.5 Discussion

In this study I present novel evidence for a signal driven by visual perception of body parts, which seem to elicit a memory trace beyond visual cortex, over somatosensory cortices (SCx). This visually driven contralateral delay activity (vdCDA) describes the involvement of SCx in encoding and maintaining visual bodily information (i.e. hand images) during a visual working memory task. Moreover, the subtraction of visual-only trials from visual-tactile trials, allowed us to identify such vdCDA in the form of an independent neural response that was evoked in somatosensory cortices during visual processing, over and above possible carryover visual effects from the visual evoked responses. The subtractive method on which this work is based has been previously employed in other event related potentials studies (e.g., Teder-Sälejärvi et al., 2002; Dell'Acqua et al., 2003). However, only recently it has been used to show visually independent somatosensory activity (Sel et al., 2014). This approach allowed us to conclude that attentional selection and encoding of body images and its modulation by load in SCx is not a mere carryover effect from similar activation patterns in visual cortices. Finally, the similar contralateral disposition of the visual and somatosensory cortices has allowed us to compute parallel subtractions to show a lateralized effect in contralateral *vs*. ipsilateral hemispheres in visual and somatosensory cortices during a visual working memory task (see Vogel and Machizawa, 2004; Katus et al., 2014).

Visual activity from visual-only trials. In congruency with previous studies (e.g., Luck and Vogel, 2013; Vogel et al., 2005; McCollough et al., 2007) arbitrary visual stimuli, such as the control geometrical shapes of the current work, elicited a similar visual contralateral delayed activation (vCDA) modulated by memory load in visual cortices. Specifically, we found an interaction of hemisphere by memory load, indicating increment of brain activity in the contralateral hemisphere to the cued

hemifield. This activity was concomitant to the increasing number of polygonal shapes to-be-remembered.

SCx activity after subtracting visual activity from visual-only trials. In the hand images stimulus conditions, we found a significant contralateral delayed activation modulated by the number of items to be maintained in working memory (load) over SCx. Such a modulation over SCx was not found when remembering the control visual stimuli (geometrical shapes). In addition to a modulation of SCx during the delayed period of the WM task, we found an earlier negativity in the time range of previously reported attentional components (i.e., n2pc, Eimer et al.,1996). This modulation was found 200-300ms after the onset of the stimuli and over the contralateral SCx. It is possible that such modulation could reflect increasing demands on focused attention.

Overall, the results of the visually driven signals vdN2cc and vdCDA over SCx exhibit novel evidence for encoding of visual information in functionally different sensory cortical regions, which match the functional and perceptual characteristics of the perceived stimuli (i.e. body images in SCx).

3.5.1 Debate on the meaning behind sustained activity and WM

The CDA, and other so called sustained, persistent, and above-threshold neural activity in working memory has also been recently target of extensive research. In particular, the CDA has been shown to reflect also selection and maintenance of object-tracking, being modulated by the quantity of objects to be tracked and correlated with ones' individual tracking capacity (Drew and Vogel, 2008). Another study examining changes in effective connectivity by the means of EEG and single pulse TMS, delivered during the delay period of a visual working memory task over superior parietal lobule, revealed higher efficiency of stimulus processing during working memory training. After training, the experimental group showed increasing

memory capacity coupled with decreasing magnitude of the CDA (Kundu et al., 2013).

Overall, these and other work (e.g, Carlisle et al., 2011) suggest that persistent neural activity (e.g., CDA) may index demands placed on attention rather than taxing pure mnemonic activity. Remembering whether the long sustained CDA or earlier components, such as our also present modulation by load (200-300ms) over SCx in the hands condition only, relate closely to a more pure attentional or mnemonic process still a work in progress. Nevertheless, from our current understanding, despite the existing diversity within working memory models (including state-based and more specifically, sensory recruitment models), all converge upon the encoding of information into working memory by activating one of the possible several states of the information. Here encoding of information in working memory occurs when activating those internal states of the information that are relevant for the task at hand, process which ultimately is based on stored representations. In these models and in consistency to our data, encoding of information in working memory occurs when activating those internal states of information that are relevant for the task at hand (D'Esposito, 2007; D'Esposito and Postle, 2015), a process which ultimately leads to stored representations. Likewise, multivariate pattern classifiers trained to predict the locations on a working memory task have been shown to cross-predict the locations on other attentional paradigms, suggesting the resemblance and correspondence of the sustained activity over cognitive tasks (Jerde et al., 2012).

3.5.2 Role of somatosensory cortex in WM for visually perceived body stimuli

Somatosensory cortices hold a specific representation of our own body (Martuzzi et al., 2014) and its role in perception (Gazzola and Keysers, 2009; Bolognini et al., 2011) and other cognitive processes (Romo et al., 2002) involving body stimuli have

recently been suggested. Importantly, our data provides the SCx with a new functional role: encoding and maintaining *visual* body information in short term memory. Consistent with our findings, current accounts in working memory have shifted from multicomponent models underpinned by highly specialised systems (Baddeley, 2003) to state-based models of working memory (D'Esposito and Postle, 2015). These later models postulate that the temporary representation of stimuli occurs in brain areas such as sensory cortices, which also process these same stimuli in the absence of working memory demands, characterizing working memory as a re-establishment of perceptual experience (Tsubomi et al., 2013; D'Esposito and Postle, 2015; Postle, 2006). Our results contribute to this account by suggesting that visually perceived information is not necessarily sustained by perceptual relevant cortices but by those that are functionally relevant.

In the present study, we speculate that SCx represents body-related stimuli or at least some of the dimensions that represent the percept in WM, and that this process is underpinned by exposition and functional associations between one's experience and others' bodies. This repeated perceptual stimulation is likely to be stored as sensory associations between the tactile sensation and the view of bodies (i.e., feeling or moving my own hands and seeing others' hands).

3.5.2.1 Further questions to be explored

One of the relevant remaining questions concerns the content representations of SCx. Specifically, what is the exact role and content of SCx in subserving mnemonic processing? SCx seems to be able to represent tactile-related content and actions that are visually perceived, resembling activity elicited when touching or being touched (Keysers et al., 2004; Kuehn et al., 2013; Nakano et al., 2012; but see touch and use of tools, Chan and Baker, 2015). Seeing similar objects that have different textures elicits cortical activity which tactile-related information can be reliably

decoded from SCx. Conversely, more 'pure visual' properties such as colour did not elicit considerable changes in SCx (Hua-Chun sun et al., 2016). Seeing hands in action while interacting with different objects elicits also SCx activity that can be decoded in a content-specific manner.

In the present study we specifically probed the state of SCx. However, there are additional brain regions that also contribute to perception of bodies and, potentially, to their maintenance in WM. Specifically, the motor cortex, which is located in the precentral gyrus has been strongly associated to the visual processing of body-related information (see meta-analyses of brain regions in action perception from Caspers et al., 2010; Molenberghs et al., 2012). Similar to the the tactile representation of the body in SCx, a motor representation of the body in the brain is organised in a contralateral manner. Both sensory and motor cortical strips are adjacent, connected, and somehow overlapped. Considering that brain areas supporting perceptual functions do also play a role in WM, motor regions may contribute to WM for visually perceived information —this latter matter will be explored in the next experimental chapter.

3.5.3 Conclusions

The findings of this study go beyond previous WM models that do not reflect on the link between perception and memory, and that consider both processes as underpinned by dedicated systems (Baddeley, 2012). We revise contemporary accounts in STM and WM based on sensory recruitment with a novel characteristic: mnemonic encoding of stimuli to-be-remembered in terms of their functional associations and not only sensory acquisition properties. In the past, visual non-body-related information showing lines, colours, or shapes (comparable to our control stimuli) has elicited activity over posterior cortices (Vogel and Machizawa, 2004;

Todd and Marois, 2004; Luck and Vogel, 2013; Vogel et al., 2005; McCollough et al., 2007; Tsubomi et al., 2013). More specifically, CDA seems to originate in visual and associated cortices (Luria et al., 2016) as shown by some studies using MEG (Robitaille, Grimault and Jolicœur, 2009; Becke et al., 2015). Tactile percepts in form of frequencies or taps elicits tactile CDA (tCDA) originated in SCx (Katus et al., 2014; Katus et al., 2015; Harris et al., 2002; Katus and Andersen, 2015; Katus and Eimer, 2015).

Our results support a more dynamic representation of the information, in which neural memory storage occurs in a content-specific rather than in a sensory-modality (based on acquisition) manner. Here, the perceptual and functional characteristics of visual stimuli rather than the sensory input modality determine how information is encoded and stored. Thus, any neural region that participates in the representation of information may maintain information in memory. Possible mechanisms behind this could be based on hebbian learning (Sandberg et al., 2003) or synaptic reweighting of sensory input. In either case, content-specific processing that is driven by functional associations results in a more suitable memory framework that eases the need of relocating relevant information to a limited number of highly specialised memory systems (Postle, 2006; D'Esposito, 2007; D'Esposito and Postle, 2015). This process seems to go over and above those sensory cortices participating in the initial acquisition of the information, being mediated by the neural underpinnings that participate in the functional encoding of the stimuli to be remembered.

In conclusion, current accounts postulate that WM is better understood as a reestablishment of perceptual experience in a 'sensory input congruent-manner' (e.g., somatosensory cortices to acquire, perceive, and also to maintain tactile stimuli in STM). However, research in the action perception domain has shown that 'bodily matters' (i.e., seeing bodies, actions, body-object interaction, etc.) engage brain

areas beyond those visual cortices used during the perceptual stage. In this first study, combining pieces of evidence from the WM and action observation fields resulted in our novel paradigm, which shows that even when a similar sensory input modality is used, engagement of sensory cortices during WM encoding depends on the nature of the stimuli to-be-remembered. A part of this novel mnemonic principle, body-related cortices seem to maintain visually acquired body stimuli in WM. Altogether, the results presented here show that WM follows also functional and not just sensory principles.

3.6 Artistic Impressions III

Left panel

Bodily Realm – Escher's allegory (2015) Photography on board (21 x 29cm) / AGP

The Method reveals that when perceiving others bodies, we seem to represent some of their components over and above visual brain areas (those ones shown in the *Visual Realm*). Others' bodies could be forged in our memories on the same regions that represent our own body.

Right panels

Portraits of thin air: AI, Duo, IR (2016) Photographs on board (29 x 29cm) / AGP

Light reflected on bodies depicting bodily representations. From encoding to functional representation reflects on the step perception of mere light to functional representations.

4. Chapter 4: Sensorimotor recruitment during WM for body and non-body-related images

4.1 Study 2: Introduction

Behavioural studies suggest the presence of a WM system contributing to memory encoding of visually perceived body information. Moreover, according to the current WM framework, areas of the brain that may contribute to such a WM system are those playing a role in perception of body stimuli. In *Chapter 3* I investigated one these neural candidates: somatosensory cortex (SCx). I applied a novel ERP-EEG method to explore SCx responses during a visual WM task where stimuli to-be-remembered were body and non-body-related images. The results showed that brain activity increased with the number of body stimuli to-be-remembered over the contralateral SCx. Visual percepts (i.e., hand images) elicited a response modulated by memory load over and above visual electrode sites, what we called visually-driven contralateral delay activity or vdCDA. This suggests memory encoding of body-related information in cortices that match the sensory features embedded in the percept.

While the study in *Chapter 3* was designed to examine activity in SCx, the present chapter explores whether or not the number of body images to be held in WM may modulate activity in motor cortex; brain region linked to perception of body-related stimuli too. To pursue this matter, I will briefly recap existing accounts in WM, as well as, those brain areas activated during perception of bodies. Secondly, I will present an ERP component associated to motor-cortical processing, and I will introduce how this component can be dissociated from concomitant activity elicited at the sight of

body stimuli during a visual WM task. Third, I will introduce the hypotheses of the study, methodological aspects, considerations, and the results of both visual and motor-cortical potentials. Last, I will discuss the present findings and review the overall limitations of this study.

4.1.1. Outline of sensory recruitment models

Expanding *Chapter 1* to *3* on the origins and characteristics of sustained activity, it refers to that neural activation classically observed when participants engage in tasks that demand continued attention and mnemonic encoding. Ruchkin et al. (1990) and Vogel and Machizawa (2004) combined this specific marker of encoding and mnemonic processing with paradigms exploiting the contralateral primary disposition of sensory cortices. Specifically, they developed a bilateral change detection paradigm similar to that used in the study of *Chapter 3*, in which participants were asked to hold in memory either the items cued in the left or right hemifield while fixating their gaze in a centred cross.

Once perceptual parameters are controlled, the hemisphere contralateral to the cued hemifield exhibits a slow negativity, which persists through the whole retention interval and increases with the number of items to be stored in WM. Conversely, the ipsilateral hemisphere exhibits activity more closely related to the perception of stimuli that are not to-be-remembered. This manipulation allows for a subtraction of activity from contralateral and ipsilateral hemispheres. Therefore this component (namely, contralateral delay activity; CDA) is supposed to reflect neural activity due to encoding and memory-only effects during experimental manipulations with increasing memory load.

As described in the previous chapter, a *tactile* contralateral delay activity (tCDA) has been described for tactile WM (Katus et al., 2014, 2015). This tCDA follows the same scheme as the vCDA: sustained activity being modulated by the quantity of

information to-be-remembered over the contralateral sensory hemisphere. The loci of such modulation is revealed when event-related potentials are locked to the stimuli onset, as well as to retro-cues indicating what tactile or visual parameters that are embedded in a given percept need to be recalled (Katus and Eimer, 2016).

Crucially, body-related brain areas do not only process tactile information in a lateralized manner, but also visually perceived body-related information. As revealed in *Chapter 3*, this allows observation of a visually driven neural signature sensitive to memory load (namely visually-driven CDA —vdCDA) that suggests encoding and maintenance of visual body-related information in areas other than visual (i.e., SCx). Relevant for the current study, motor cortex also process visually perceived body stimuli in a contralateral manner in both perceptual and actual motor domains (e.g., seeing hands and one's hands). The following section summarises brain regions activated during perception of action and bodies.

4.1.2. Outline of sensorimotor involvement during perception of bodies

Motor areas are predominantly found in Brodmann areas 4, 6, and 8 over frontocentral and frontal cortices. Compared to SCx, which is located over the postcentral gyrus, primary motor cortex is located on the anterior verge of the central sulcus. Although motor production is the characteristic purpose of these regions, sensory stimulation also elicits responses in such brain areas. More precisely, recent papers suggest robust interactions between 'purely' motor areas and SCx in learning motor skills through observation (Lametti and Watkins, 2016). From posterior to anterior, the next brain region is the premotor cortex, which extends to the medial longitudinal fissure. This region is responsible for the guidance and control of body movements. Activity in premotor areas has been observed in tasks involving observation of bodily actions, as well as actions requiring imagining and preparing movements (Kranczioch et al., 2009, 2010; Grosbras et al., 2012). The anterior part

of the supplementary motor area (SMA) is curiously more active when imagining movements whereas the posterior and caudal region are more active during execution (Stephan et al., 1995; Grafton et al., 1996). Lastly, in a more anterior location, frontal eye fields have been associated to imitating, maintaining, and coordinating ordinal movements, as well as rehearsal of motor repertoires (Rizzolatti et al., 2002; Nachev et al., 2008)

Overall, a distributed network of brain areas, including the aforementioned plus other regions such as inferior parietal lobe and superior temporal sulcus, comprise brain systems partially overlapping and contributing to both perception of bodies and execution of one's movements (Kilner, 2011), as well as, functions related to visuomotor processing and acquisition of motor skills (Sakai et al., 2002; Grèzes et al., 2003). Strong evidence for the resemblance between perception and motor components within the motor areas comes from fMRI studies including sensorimotor experts viewing actions (Calvo-Merino et al., 2005, 2006; Pilgramm et al., 2010; Kim et al., 2011), sensorimotor imagery studies (Lotze et al., 1999; Fourkas et al., 2008), and studies on simulation (Cross et al., 2006). Altogether, encoding of body-related information follows functionally discrete and spatially overlapping regions that are relevant for encoding others' bodies and actions (Jacquet and Avenanti, 2015).

Besides the aforementioned fMRI studies, an EEG component associated to motor processing and source localized over motor regions has been thoroughly investigated (i.e., readiness potential). This component has been mostly associated to motor execution. However, some studies have shown that the readiness potential also reflects visually perceived body-related information. In principle, it seems possible to borrow such a component, adapting it to the study of WM for visual processing of body images. In the following section I introduce how the readiness potential is elicited, its temporal dynamics, and its neural generators.

4.1.3. Measuring motor processing by means of motor-cortical potentials

The Bereitschaftspotential or readiness potential (RP) (Deecke et al., 1976; Shibasaki and Hallett, 2006; Smulders and Miller, 2012) refers to a movement-preceding negativity that originates in motor cortices before a movement is implemented (Cunnington et al., 2003). The RP has been classically understood as an indicator of preparation for self-initiated and goal-directed upcoming movements (Shibasaki and Hallett, 2006). The RP is normally elicited by asking participants to perform/execute simple finger or arm movements and it is normally recorded through EEG. The RP could be considered within the family components of motor-cortical potentials (MCPs).

According to the RP's time course and source localization, two different periods can be distinguished: first, the RP appears as a steady bilateral activity that can be source localized over SMA. Second, it lateralizes over the motor cortices of the effector in the task around 300-500ms before the actual onset of the movement (Deecke et al., 1976; Cui and Deecke, 1999; Rueda-Delgado et al., 2014) (Fig. 4-1). These lateralized components are well known in their isolated version: the lateralized RP. In unilateral motor responses, structural and functional interhemispheric asymmetries are deducted by computing a double ERP subtraction between mean amplitudes (De Jong et al., 1988; Eimer and Coles, 2003). The subsequent lateralized readiness potential (LRP) amplitude is modulated by several factors such as the force, intention, or the complexity of forthcoming action (e.g., finger movements) (Cui et al., 2000a, 2000b) whether these are executed or imagined (Kranczioch et al., 2009, 2010).

Another component of interest is the contingent negative variation (CNV), which can be measured from the onset of a warning stimulus to a forthcoming imperative

second stimulus involving a certain response. The CNV has been associated to orienting and expectancy towards a given signal (Leuthold et al., 2004; Leuthold and Jentzsch, 2009). Even though the CNV looks very similar to the RP and it engages similar neural generators, the RP is more lateralized, it requires motor response, and it is normally observed in the absence of external imperative stimuli. Remarkably, the lateralization of the RP seems to happen when participants decide consciously to perform a body movement (Trevena and Miller, 2002). An evident difference between RP and CNV is that the latter is expected to involve neural generators contributing to additional cognitive processes. Specifically, the later part of the wave of the CNV can be movement-related, as well as related to perception and other processes such as memory and attention (Smulders and Miller, 2012; Rueda-Delgado et al., 2014). The mix of cognitive processes found in the CNV is due to processing of the upcoming warning stimulus and the preparation of the movement to be implemented. Nevertheless, if a fast response is required in a CNV task, this activity would resemble that of the late RP: a response parameter associated with motor processing, involving sensory and motor associations that can be modulated by external factors inherent to the requirements of the task at hand (Frost et al., 1988; Leuthold and Jentzsch, 2009; Brunia et al., 2012).

Relevant for the present study is the variant of both aforementioned components: the cued motor-cortical potential. Compared to the volitional RP, this motor preceding negativity is elicited by explicitly asking participants to execute a movement. In comparison to other motor-cortical potentials (MCPs), it is very similar to the RP and the late portion of the CNV. In the specific case of the RP, both the cued MCP and the traditional RP possess similar latencies but the cued MCP involves additional activation from lateral premotor cortex (Smith and Staines, 2012).

Despite MCPs having been normally associated with goal-directed bodily actions, the requirement of sensorimotor activity as arising inly prior to motor execution is debated. For instance, listening to 'do and don't do' abstract or action-related sentences activates the motor regions, reflecting different modulations between positive and negative action-related sentences compared to abstract ones across fronto-parietal cortices (Tettamanti et al., 2008). An EEG study showed that volitional non-actions (i.e., choosing not to act), elicits ERPs comparable to those observed during volitional and instructed acts (Kühn et al., 2009). Another EEG study, Alexander et al. (2016) compared volitional decisions with and without motor responses, showing a similar RP regardless of the presence of the actual motor response. These authors argue in favour of the RP as a neural signature reflecting decision-related processes instead of purely motor activity. Direct recording of neural activity in the premotor cortex of the macaque monkey has shown that neurons respond to both acting and non-acting (i.e., refraining from doing it) and that some these neurons fire when particularly observing others in either one of these two motor conditions (Bonini et al., 2014).

Overall, MCPs studies suggest that: i) sensorimotor cortices do not strictly support information-representation of the forthcoming movement. Instead, they seem to reflect the motor consequences of an act whether this is executed or not (i.e., the consequences of an action not to be performed). ii) This idea is strikingly similar to Prinz's work (Prinz, 1997; Schütz-Bosbach and Prinz, 2007), which tied perception of events to the motor consequences embedded in them. This postulate implies the use of stored associations and representations to guide future behaviour. iii) Supporting this, predicting others' actions during action observation modulates the readiness potential (Pineda et al., 2000; Kilner et al., 2004; van Schie et al., 2004). Thus, motor cortices seem to play an important role in processing visual information related to

others' bodies and actions. Similar to *Chapter 3*, this visual to sensorimotor transformation allows the possibility of measuring visually driven processing of body-related stimuli during their maintenance in cortices other than visual (i.e., motor).

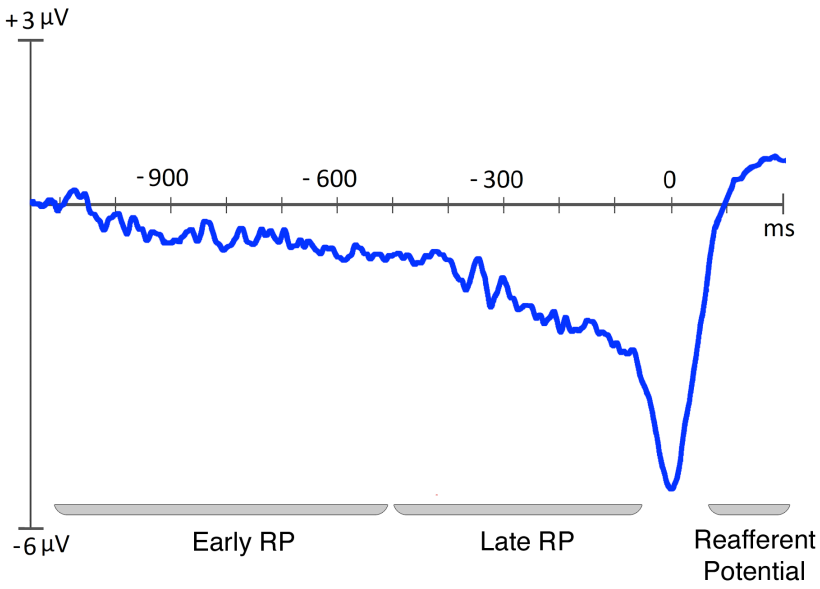


Figure 4-1. Illustration of readiness potential waveform. Considering time-course, slope, and sensory generators, three periods have been generally identified: early RP develops until -500 to -300ms before movement onset (central, bilateral). Late RP develops until movement onset, generally includes the half second before movement onset to -80 or to 0 ms (zero indicating participants' actual motor response) (contralateral to the effector). A reaffererent potential in the form of a positive peak is generally observed around 150-200ms after movement onset. Positive ERP waveform plotted upward.

4.2 Aims, method development, and predictions

4.2.1 Concatenating concepts

In this *Chapter* there are four different pieces of evidence that need to be considered: 1) the resemblance between perceptual and WM mechanisms (D'Esposito and Postle, 2015), 2) the contribution of motor cortex in processing visual information regarding body-related stimuli, 3) the existence of an EEG component (readiness potential) reflecting the state and underlying processing of the motor cortex, and 4)

the overlap between some of the neural generators reported in fMRI studies of action perception and EEG studies using the readiness potential (Fig. 4-2).

Aims of the study. In the current experiment, we explore if encoding and maintenance of non-body and body-related stimuli elicits persistent activity in motor cortex, which participates in processing the latter stimuli in the absence of WM demands. More specifically, we examine whether or not the type and number of stimuli to-be-remembered involves recruitment of motor cortices. This would exhibit an enhancement by memory load of the ERP waveform over motor cortex. Such a result would also support sensory recruitment models of WM (Pasternak and Greenlee, 2005; Serences et al., 2009; D'Esposito and Postle, 2015), suggesting encoding of visual information in distinctive cortical regions that match the characteristics of the stimuli to-be-remembered, a process that it is known to delineate perception of bodies and actions.

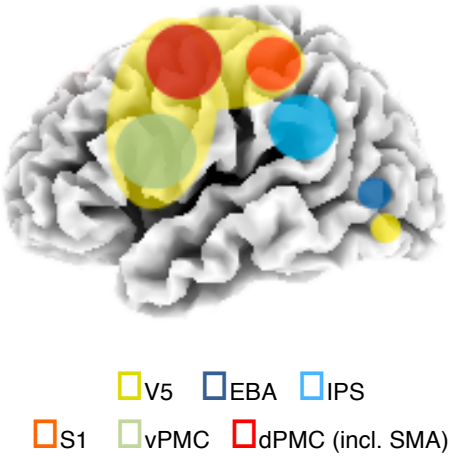


Figure 4-2. Schematic illustration of overlapping brain regions in studies of RP and action perception. Coloured circles cover brain regions contributing to action perception. Yellow shadow covers brain regions that are also modulated in studies of RP. EBA: extrastriate body area; S1: primary somatosensory cortex; vPMC: ventral premotor cortex; dPMC: dorsal premotor cortex; IPS: intraparietal sulcus; SMA: supplementary motor area.

Methodological approach. To address our aims, we developed a novel paradigm inspired by that proposed in *Chapter 2* and used in *Chapter 3.* This paradigm enables dissociating visual processing from visually driven activity in brain areas beyond visual cortex (i.e. in motor cortices). This paradigm takes advantage of two major neural features: the lateralized organization of sensory systems, and the use of stimuli that differ in the type of processing that they evoke (non-body and body-related stimuli).

We recorded both visual and motor-related cortical potentials while participants performed a visual WM task in which stimuli to-be-remembered were hand images depicting different hand positions and analogous geometrical shapes. We computed the aforementioned vCDA, as well as recorded cued motor-cortical potentials (MCPs) during the retention interval of each trial. Cued motor-cortical potentials (MCPs) are closely related to the volitional readiness potential or Bereitschaftspotential (Deecke et al., 1976; Shibasaki and Hallett, 2006). This multifaceted component arises from frontal and motor cortices and reflects underlying processing of one's motor responses (e.g., forthcoming complexity of an executed or imagined action; (Kranczioch et al., 2009, 2010) and others' observed bodily actions (van Schie et al., 2004).

The key factors of this experiment included: stimulus type (hand, shape images), memory load (1, 2 images), and hemisphere (ipsilateral, contralateral). These factors were computed in the analyses of visual-evoked potentials and motor-cortical potentials after subtraction of visual carry-over effects; VEPs and MCPs, respectively.

Predictions. By developing a WM paradigm comprising both visual and motor cortical-potentials, we sought to examine effects of memory load across visual and motor brain regions. We predicted that once dissociated from visually elicited activity

in the same WM task, MCPs arising from engagement of motor areas would reflect increasing activity depending on the number of body-related images to-be-remembered (i.e., enhanced brain activity when remembering one hand image compared to two hand images over motor electrode sites). This would exhibit novel evidence for neural recruitment in functionally different sensory cortical regions that match the perceptual and functional characteristics of the perceived stimuli. Therefore, with our design and methodology, we expect to identify a novel signature that represents the encoding of visual percepts beyond the expected early visual processing.

4.3 Methods

Participants

Twenty participants (10 females; mean age = 29) with normal or corrected-to-normal vision took part and gave informed consent for this study, approved by City, University of London Psychology Department's Research Ethics Committee. The sample size was chosen based on related studies and paradigm (Vogel and Machizawa, 2004; Katus et al., 2015)

Stimuli

A set of 6 pictures of right hands depicting different hand postures and finger positions with no meaning or symbolism was used. These hands were horizontally rotated to the left, obtaining 6 pairs of right and left hands that were then greyscaled. In parallel we created a control condition based on a set of geometrical shapes matching the hands' outline, size, and colour.

Experimental design and procedure

Participants were seated in front of a LCD monitor (75 Hz) in a dimly lit, electromagnetically shielded room. Participants' forearms rested on the top of a table

with their hands separated about 25cm, in palm down position, and covered by a black opaque surface.

Participants performed both stimuli conditions (i.e., hand and geometrical shapes) in counterbalanced order. They were instructed to recall differences between pairs of arrays depicting different hand postures or shape forms. At the beginning of each trial a central arrow cue (200ms) instructed the participants to covertly attend to the items in either the left or the right hemifield. After the offset of the arrow cue (300-400ms), the memory array was displayed for 100ms and followed by a blank retention interval (800ms). At the end of the retention interval the fixation cross changed from red in colour to green until the end of the trial, 100ms later the test array was displayed. In half of the blocks participants were instructed to ignore this colour change while in the other half and at the beginning of the corresponding blocks, they were instructed to prepare and produce a task-irrelevant motor response at the onset of the green fixation cross. This response was done by simultaneously pressing two different keys with the index fingers of both hands. Finally, the test array was displayed until participants' verbally responded whether or not the stimuli in the cued hemifield of the test array were identical to those in the memory array. One of the items in the test array differed from the memory array in 50% of the trials; the rest of the stimuli remained the same. All trials were separated by a 700ms blank interval.

Shapes and hands stimuli were displayed using E-Prime Software (Psychology Software Tools). All stimulus arrays were presented within two 4.5° x 8.5° rectangular regions that were centred 5° to the left and right of a central fixation cross on a grey background. Each memory array consisted of 1 or 2 hands (1.3° x 0.8°) in each hemifield, each stimulus randomly selected from the set of twelve hands. Right hands were shown on the right hemifield while left hands were displayed on the left. The rationale behind this choice is based on the clear contralateral representation of the

hands in the motor cortex. This allows observing contralateral activity over motor regions that can be dissociated from concomitant visually evoked activity when seeing and remembering the stimuli. In the control condition 1 or 2 polygonal shapes (1.3° x 0.8°) were selected and shown in a similar fashion. The positions of all stimuli were randomized on each trial with the restriction that distance between stimuli within a hemifield was maintained to a minimum of 2.4° (centre to centre).

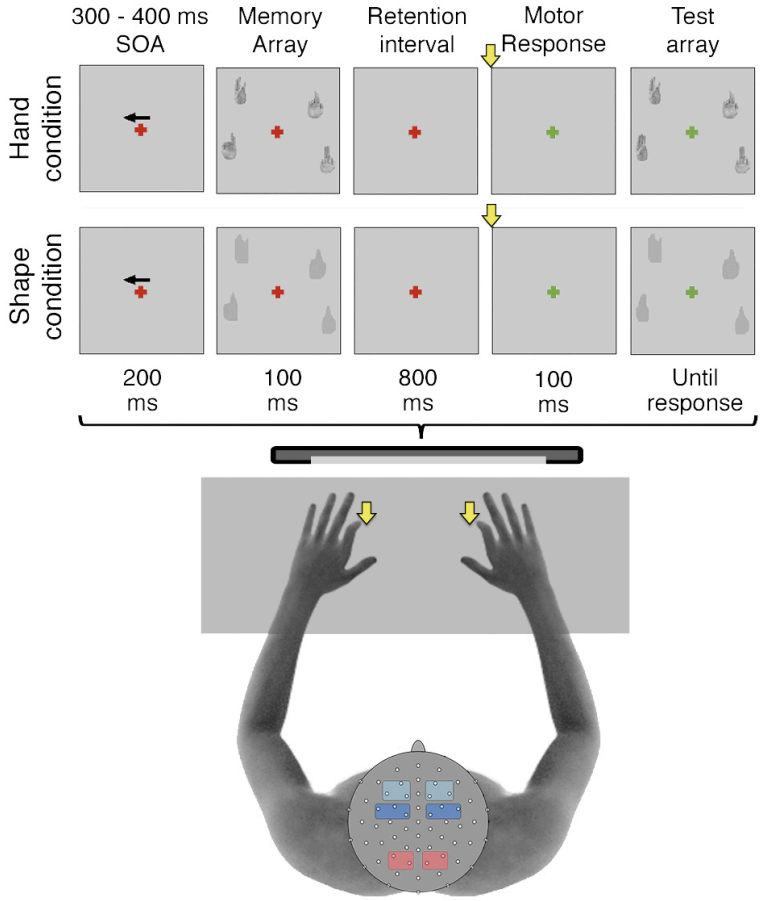


Figure 4-3. Task design and procedure study 2. Illustration of trial displaying memory load 2, cued to the left hemifield, in hand and shape stimuli conditions (participants performed both stimuli conditions in counterbalanced order). On half of the trials, participants performed a task-irrelevant motor response by simultaneously pressing two different keys with both index fingertips at the onset of the green fixation cross array (yellow triangles). Participants verbally responded whether the memory array and test array were the same or different. Electrode map shows electrodes over visual (red) and motor ROIs (blue). SOA: stimulus onset asynchrony.

Since previous studies have shown that holding in WM 2 items may well lead to limits in WM capacity (Alvarez and Cavanagh, 2004; Olsson and Poom, 2005; Luria et al., 2010); memory load 1 and 2 would allow detecting increasing activity related to memory encoding and maintenance of the stimuli. During the experiment, the presentation of the stimuli and tasks was blocked: In counterbalanced order, half of the participants started by completing the hand stimulus condition while the other half started by the shape stimulus condition. We also counterbalanced those trials in which participants were asked to exert an irrelevant motor response (visual-motor condition). Specifically, visual and visual-motor trials were counterbalanced across entire blocks of 84 trials. The number and specific type of stimulus from the stimulus sets were randomly selected. Overall, participants performed a total of 1344 trials, 672 for each stimulus condition (hands and geometrical shapes). This is equal to 336 trials for each memory load condition (load 1 and 2).

EEG recording and data analysis.

EEG was recorded with active electrodes from 64 scalp electrodes mounted equidistantly on an elastic electrode cap (M10 montage; EasyCap). Electrodes were referenced to the right mastoid and re-referenced to the average reference off-line. Vertical and bipolar horizontal electrooculogram was recorded for eye movements tracking and artifact correction purposes. Continuous EEG was recorded using a BrainAmp amplifier (BrainProducts; 500 Hz sampling rate). Off-line EEG analysis was performed using Vision Analyzer software (BrainProducts). The data were digitally low-pass-filtered at 30 Hz, and ocular correction was performed (Gratton et al., 1983). Trials with horizontal eye movements (HEOG exceeding ± 55 μV) or other artifacts (voltage exceeding ± 85 μV at any electrode) were excluded from analyses. The EEG signal was epoched into 1750ms segments, starting 200ms before the sample array of each trial and ending 550ms after the onset of the green fixation

cross. This included stimulus-locked potentials in the visual-only condition and both stimulus-locked and response-locked potentials elicited by the irrelevant-task motor response in the visual-motor condition. Importantly, all segments were then baseline corrected to the first 100ms. Following this, segments comprising stimulus-locked potentials were epoched into 1200ms and segments comprising response-locked potentials were epoched into 1250ms (-1150ms preceding the motor response to 100ms after).

Stimulus-locked potentials: Grand averages were computed independently for the two stimuli conditions, separately for the two memory loads, and for visual-only trials by averaging brain waveforms elicited at electrodes over the hemisphere contralateral and ipsilateral to the side to be memorized as indicated by the central cue. Then, visual contralateral delay activity (vCDA) was computed from 300 to 800ms after the onset of the stimuli to be remembered as the difference between contralateral amplitudes (averaging evoked potentials over right visual hemisphere when attending left hemifield and over left visual hemisphere when attending the right hemifield) and ipsilateral amplitudes (average of evoked potentials over the right visual hemisphere when attending the right hemifield and *vice versa*) (Luck, 2012). Statistical analysis was performed for mean amplitudes in accordance with sites and time windows reported in previous studies, specifically, occipital and posterior parietal electrode sites (midway between POz and PO3, midway between PO7 and P3 / midway between POz and PO4, midway between PO8 and P4 of the 10-20 system) (Luck et al., 1993; Vogel and Machizawa, 2004; Vogel et al., 2005).

Response-locked potentials: Motor-related cortical potentials (MCPs) reflect processes involved in movement planning, observation, execution, and motor learning. Previous studies describe a steep negativity approximately half a second before onset of voluntary movements which is found over the contralateral M1 cortex

of the moving hand. The cued MCP employed in the present study is somewhat similar to the volitional Bereitschaftspotential (Deecke et al., 1976; Brunia et al., 2012): It follows similar temporal dynamics, however, it involves additional activation over premotor areas.

MCPs were obtained by averaging the elicited activity preceding the irrelevant-task motor response in the visual-motor condition, meaning that they were measured with respect to the moment the participants performed the motor execution (from -1150 to 100ms, 0ms being the actual motor response). We then computed statistical analysis of MCPs that allowed us to explore our main hypothesis: neural recruitment of brain regions matching the perceptual and functional characteristics of the perceived stimuli (i.e., sensorimotor regions modulated by the number of hand images to-be-remembered). To this aim, we averaged contralateral MCPs (averaging brain activity over right motor hemisphere when attending left hemifield and over left motor hemisphere when attending the right hemifield) and ipsilateral amplitudes (average of evoked potentials over the right hemisphere when attending the right hemifield and *vice versa*). In accordance to the aforementioned temporal dynamics, as well as electrodes sites used in previous research (Kranczioch et al., 2009; Smith and Staines, 2012), we defined two regions of interested (ROI) that were analysed from -500ms to -50ms before the onset of the movement produced in the task-irrelevant motor response. There were two hemisphere factors (contralateral and ipsilateral) and two ROIs: frontocentral (midway between C1 and FC1/midway between C1 and FC2, FC3/FC4, FC5/FC6) and frontal (F1/F2, F5/F6, and AF3/AF4). All the factors included in the analyses were hemisphere (contralateral, ipsilateral), ROI (frontocentral, frontal), channel (3 electrodes), memory load (1,2), and stimuli types (hand, shape images). In regards to the electrode sites, note that different studies have used various arrangements. Sommer et al. (1994) recorded RP at 2, 4, and 6

cm from Cz (lateralized), as well as in more posterior and anterior electrode positions. They found fairly similar activity across electrodes with mean amplitudes differencing from zero (no differences). These results suggest that positioning of the electrodes is not very critical (Smulders and Miller, 2012)

Importantly, to deduct visual effects over more frontal and motor cortices, we imported individual markers from participants' motor responses in trials of the response-locked potentials of the visual-motor condition to the corresponding segments of the visual-only condition. By doing this we created 'virtual markers' in the visual-only condition at the estimated timing in which a motor response in the visual-motor task was done. Then, activity from visual-only trials locked to this virtual response was subtracted to the mean amplitudes of visual-motor trials (containing both motor and visual evoked potentials). This process provided us with motor cortical potentials from which visual activity spreading from more posterior areas was subtracted. This methodology is based on previous studies examining integration as well as dissociation of brain activity from distinct sensory modalities (Talsma and Woldorff, 2005; Senkowski et al., 2007; Talsma et al., 2010; Sel et al., 2014) and a more recent study examining motor activity linked to decision and volitional processing of movement (Alexander et al., 2016)

Lastly, in all analyses, Mauchly's W was computed to check for violations of the sphericity assumption and Greenhouse–Geisser adjustments to the degrees of freedom were applied when appropiate. The P values were corrected for multiple comparisons using Bonferroni correction.

Electrophysiological source localization. Based on the scalp-recorded electric potential distribution, the Standardised Low Resolution Brain Electromagnetic Tomography (s-LORETA) (Pascual-Marqui et al., 1994; Pascual-Marqui, 2002) was used to estimate the brain generators associated with modulations by memory load

between stimuli types in MCPs. Specifically, the differential activity between the hand and shape stimuli conditions in the time window from -500 to -50ms of the MCPs after subtraction of visual-only trials' activity was subjected to source localization. sLORETA provides an approximate three-dimensional discrete solution to the inverse EEG problem. It estimates the most active brain areas using a 5mm resolution brain volume template of the Montreal Neurological Institute (MNI). MNI coordinates were translated to Talairach coordinates by Talairach Daemon. Compared with other dipole-based methods, s-LORETA has the advantage of estimating activity sources without any a priori assumptions about the number of sources or their location.

4.4 Results

4.4.1 Behavioural results

In the shapes stimulus condition, participants correctly reported differences or similarities between the memory and test array in 78% of all trials in the visual-only condition and in 73.5% of all trials correct in the visual-motor condition. Very similar performance followed the hands stimulus condition with 77% of all trials correct in the visual-only and 73% of all trials in the visual-motor condition. Performance was analysed using the sensitivity index d', which considers false alarms and hit rates, representing a more precise measurement of signal detection than percentage of correct trials only. Repeated measures ANOVA with factors stimulus type (shapes versus hands), task (visual-only versus visual-motor), and memory load (1 versus 2) showed main effects of task ($F_{(1,19)} = 52.127$, $p < 0.001$) and load ($F_{(1,19)} = 238.249$, $p < 0.001$), as well as a significant interaction of stimulus type and load ($F_{(1,19)} = 6.718$, $p = 0.018$). We followed up this stimulus type by load interaction by separately comparing stimulus type for load 1 and load 2. No significant differences between stimulus type were found for either memory load ($t_{(1,19)} = 1.105$, $p = 0.283$ and $t_{(1,19)} = -1.554$, $p = 0.137$, respectively). No significant interaction of stimulus type X task X

load was found ($F_{(1,19)} = 0.236$, $p = 0.633$) (Fig. 4-4). We also examined the reaction time needed for the bi-manual task-irrelevant motor response, which was measured from the change of colour in the fixation cross (Fig. 4-3). Overall, participants pressed after 253.5ms in the shape stimulus condition and 254ms in the hand condition. Analysis of variance yielded no significant differences between stimulus type and memory load ($F_{(1,19)} = 0.835$, $p = 0.372$). Participants consistently took slightly longer to exert the motor response when holding in memory two stimuli, a significant main effect of load was found ($F_{(1,19)} = 19.538$, $p < 0.001$). Overall, performance was very similar in the hand and shape conditions, it was equally modulated when the trial included the motor response in the form of a task-irrelevant key pressing during the retention interval of the stimuli to be remembered.

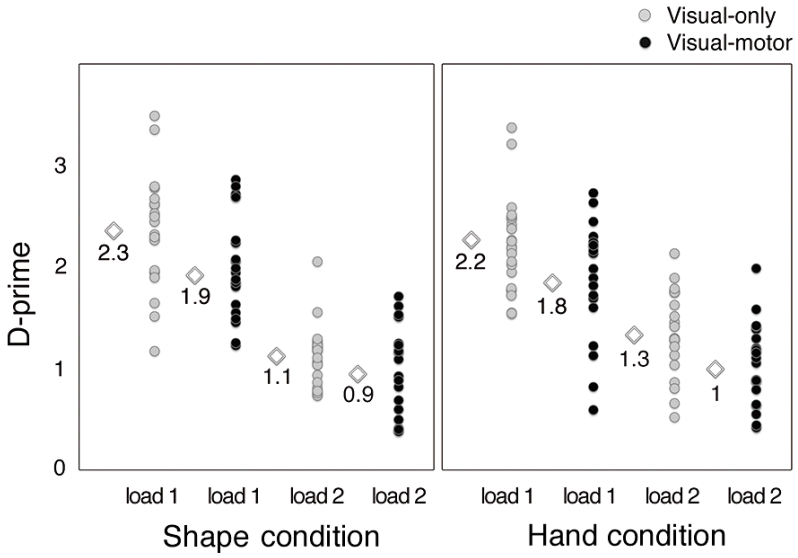


Figure 4-4. Behavioural results in visual and visual-motor conditions. Dots represent the means of individual participants; the diamond shapes the sample average. Overall performance in hand and shape conditions was similar and no significant interactions were found between performance for memory load 1 and 2 in the hand and shape conditions (all *Ps* ≥ 0.05), *n*=20. D-prime: sensitivity index, d' = Z (hit rate) – Z (false alarm rate).

Moreover, given the subtractive nature of our methodology, it is possible that variance in the signal-to-noise ratio in the subsequent conditions could bias our analyses and results between stimuli types. To rule out this possibility, we also examined the number of accepted trials separately for trials cued to left and right hemifield, for each memory load and type of stimuli in the *visual-motor* and *visual-only* task conditions. The only significant results were found as main effects of task (visual-only, visual-motor) ($F_{(1,19)} = 5.695$, $p = 0.028$) and load (1,2) ($F_{(1,19)} = 123.394$, $p < 0.001$). No effects of cue ($F_{(1,19)} = 0.780$, $p = 0.388$), stimuli types ($F_{(1,19)} = 0.633$, $p = 0.436$), nor other significant interactions between factors were found; quadruple interaction ($F_{(1,19)} = 0.445$, $p = 0.513$). These results denote that signal-to-noise ratio did not bias the results on later subtractions across stimuli conditions. Dissimilarities of mean amplitudes over sensorimotor regions sites would be likely due to effects of memory load and processing visual information conveying distinctive properties (body and non-body-related).

4.4.2 Visual recruitment: stimulus-locked potentials from visual-only trials

Visual evoked-potentials elicited at posterior parietal and occipital electrode sites contralateral and ipsilateral to the cued hemifield were analysed for both memory loads and stimuli types. Approximately 300ms after the onset of the visual arrays, a sustained negativity appeared over visual cortices. This contralateral delayed activity (vCDA) persisted across the retention interval and increased with the number of images to be remembered. We examined this activity across memory loads by subtracting waveforms from the ipsilateral hemisphere to the cued hemifield to the contralateral hemisphere (Fig. 4-5). This latter step is assumed to remove nonspecific bilateral contributions of brain activity (Luck et al., 1993; Luck, 2005). We

then computed repeated-measures ANOVA for both stimuli types with hemisphere (contralateral, ipsilateral) and memory load (1, 2) as factors.

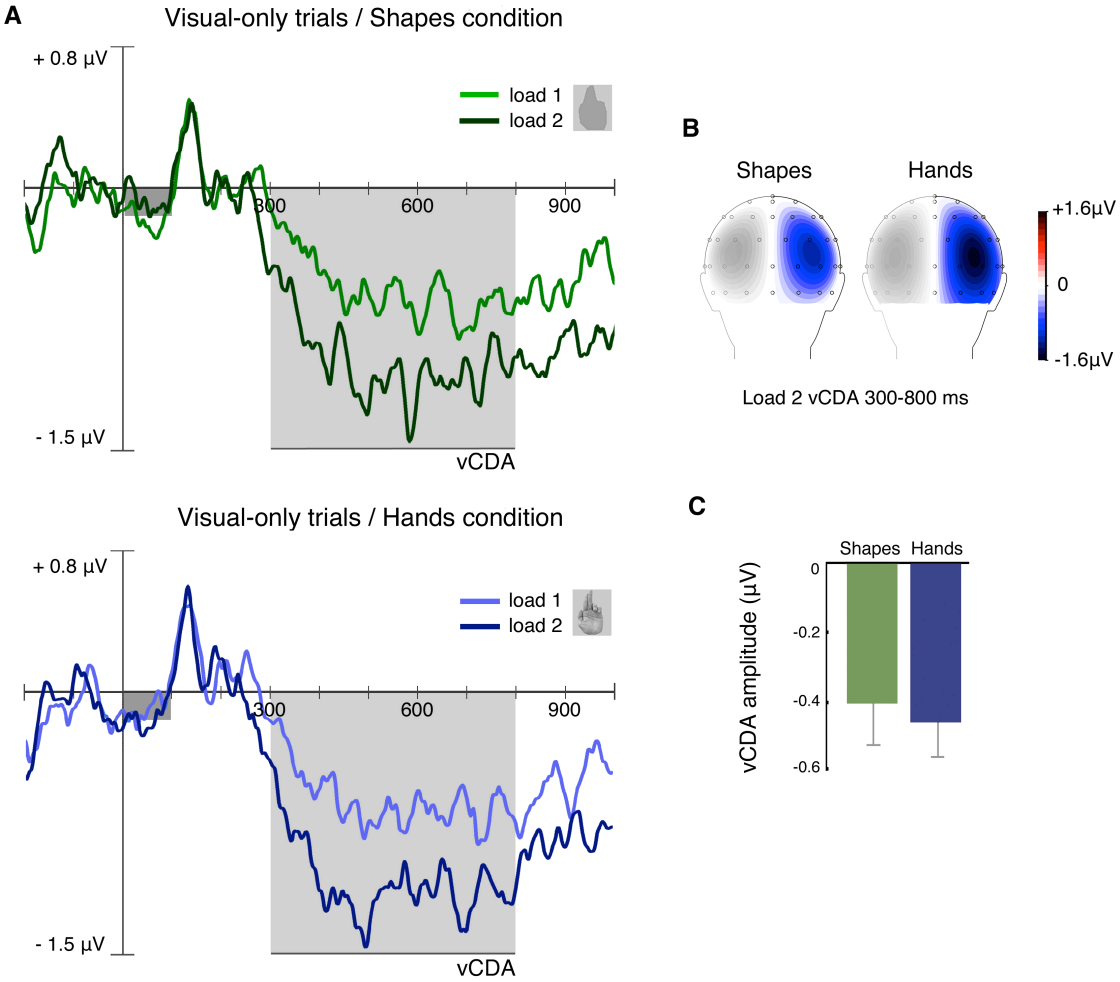


Figure 4-5. Results of stimulus-locked visual potentials. *(A)* Contralateral minus ipsilateral visual-evoked potentials pooled over lateral occipital and posterior parietal electrodes for each memory load and stimuli conditions. Analysis of variance yielded a significant difference between memory loads 1 and 2 in both stimuli conditions. *(B)* Topography of the vCDA after onset of the memory array in load 2, showing an occipital-parietal peak in the time window 300-800ms. Topographical maps show contralateral minus ipsilateral amplitude differences projected on the right hemisphere. *(C)* Differential activity between contralateral minus ipsilateral activity in load 2 minus load 1 for both stimuli conditions. Error bars represent within subject SEMs. Large grey squares indicate time windows for statistical analyses; n=20; positive ERP waveforms plotted upward

In the shape stimulus condition, the interaction hemisphere by load yielded a significant main effect of memory load ($F_{(1,19)} = 9.101$, $p = 0.007$), hemisphere ($F_{(1,19)} = 21.679$, $p < 0.001$), as well as a significant interaction between load and hemisphere ($F_{(1,19)} = 6.742$, $p = 0.018$). We followed up this interhemispheric modulation by comparing differences in mean amplitudes within hemispheres between load 1 and 2 conditions. In the ipsilateral hemisphere, differences were found between maintaining 1 and 2 in WM ($t_{(19)} = 2.149$, $p = 0.045$). In the contralateral hemisphere, differences in mean amplitudes were also found when maintaining 1 and 2 images of shapes ($t_{(19)} = 3.425$, $p = 0.003$).

Similar to the analyses of visual evoked-potentials in the shape stimulus conditions, we analysed the mean amplitudes evoked by hand images. We also found an on-going negativity arising approximately 300ms after the onset of the images to be remembered. Repeated-measures ANOVA with hemisphere and load as factors yielded significant main effects of load ($F_{(1,19)} = 9.899$, $p = 0.005$) and hemisphere ($F_{(1,19)} = 26.815$, $p < 0.001$), as well as a significant interaction between load and hemisphere ($F_{(1,19)} = 11.552$, $p = 0.003$). As we did in the follow up of such interaction in the shapes stimulus condition, we proceed to compare differences within each hemisphere's activity during maintenance of 1 or 2 stimuli. In the ipsilateral hemisphere, no differences of in mean amplitudes were found ($t_{(19)} = 1.783$, $p = 0.091$). Conversely, in the contralateral hemisphere we found a significant difference between holding in WM 1 or 2 stimuli ($t_{(19)} = 3.818$, $p = 0.001$). Overall, the vCDA, a neural marker indexing maintenance of information in visual WM (Tsubomi et al., 2013) was similar across stimuli types.

4.4.3 Sensorimotor recruitment: response-locked potentials from visual-motor trials

To examine brain activity from neural responses within motor regions in the visual WM task, over an above potential visual effects leaking from posterior to more frontal areas of the brain comprising motor regions, we subtracted mean amplitudes of visually elicited activity (visual-only trials) from mean amplitudes including both visual and motorically elicited cortical potentials during the same experimental session (visual-motor trials) (Fig. 4-6). As recent WM models postulate, if perceptual areas of the brain are involved in both perceptual and mnemonic processing, motor-related cortices (known to participate in perception and representation of bodily information) would reflect differences of mean amplitudes modulated by the quantity of body-related information to be held in WM (memory load in the hand stimulus condition).

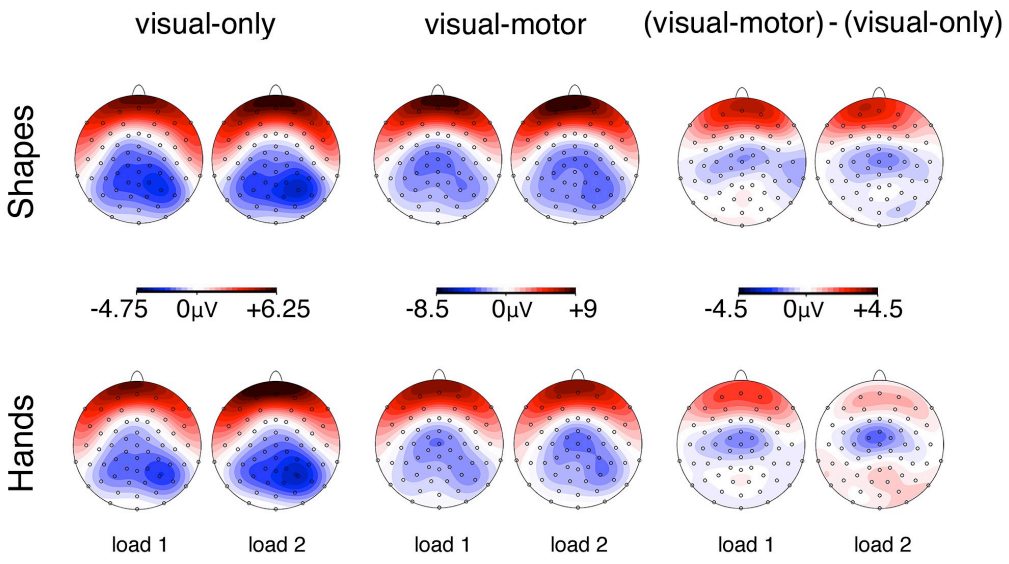


Figure 4-6. Response-locked potentials (-500 to -50ms). Whole topographical maps in all conditions, including task, memory load, stimuli types, and the subtraction from visual only trials' activity to visual-motor trials' brain activity.

MCPs in form of the canonical and sharp preceding motor negativity were clearly visible over frontocentral and frontal regions in both stimuli conditions. We computed mean amplitudes after deduction of visual activity from visual-only trials to visual-motor trials in the time windows from -500 to -50ms. MCPs elicited at motor electrode sites contralateral and ipsilateral to the cued hemifield were analysed for both memory loads and stimuli types across frontocentral and frontal ROIs. Specifically, a repeated measures ANOVA with hemisphere (contralateral, ipsilateral), memory load (1,2), stimuli types (hand, shapes), ROIs (frontocentral, frontal), and channel (3 electrodes) yielded main effects of ROI ($F_{(1,19)}$ = 32.251, $p < 0.001$) and channel ($F_{(1,19)}$ = 10.149, $p = 0.002$), significant double interactions between stimuli and hemisphere ($F_{(1,19)}$ = 4.931, $p = 0.039$), hemisphere and channel ($F_{(1,19)}$ = 4.979, $p = 0.012$), load and ROI ($F_{(1,19)}$ = 8.906, $p = 0.008$), and significant triple interactions of load x hemisphere x ROI ($F_{(1,19)}$ = 6.769, $p = 0.018$) and stimuli x hemisphere x channel ($F_{(1,19)}$ = 4.630, $p = 0.027$). Crucially, we also found a significant interaction between all factors ($F_{(1,19)}$ = 5.995, $p = 0.005$).

We followed up the latter interaction by analysing separately brain activity in each hemisphere. In the ipsilateral hemisphere we found main effects of ROI ($F_{(1,19)}$ = 28.962, $p < 0.001$) and channel ($F_{(1,19)}$ = 9.122, $p = 0.003$). The factor type of stimulus did not reach significance ($F_{(1,19)}$ = 3.362, $p = 0.082$). No additional significant effects and interactions were found. In the contralateral hemisphere, we newly found main effects of ROI ($F_{(1,19)}$ = 34.451, $p < 0.001$) and channel ($F_{(1,19)}$ = 11.392, $p < 0.001$). Interestingly, results showed a marginal interaction between stimuli and ROI ($F_{(1,19)}$ = 4.209, $p = 0.054$), which reached significance when interacting with load: stimuli types x ROI x load ($F_{(1,19)}$ = 6.046, $p = 0.024$).

Given this interaction over the contralateral hemisphere between stimuli types, ROI and load, we proceed to examine the modulation of memory load by ROI for each

stimulus type. For shape stimuli, no main effect of load ($F_{(1,19)}$ = 0.093, P = 0.763) or interaction between load and ROI ($F_{(1,19)}$ = 0.162, p = 0.692) were found. The results only showed a main effect of ROI ($F_{(1,19)}$ = 58.942, $p < 0.001$), indicating a significant difference between the frontocentral and more frontal ROI regardless of memory load ($t_{(1,19)}$ = 7.678, $p < 0.001$). Contrary, maintaining hand images in WM elicited mean amplitudes that were distinctively modulated across ROIs ($F_{(1,19)}$ = 13.573, $p < 0.002$) depending on the number of images (i.e. hands) to be remembered ($F_{(1,19)}$ = 20.811, $p < 0.001$). Follow up of analyses separated by ROIs showed a significant difference of mean amplitudes in the frontal ROI when holding one hand *vs.* two hands ($t_{(1,19)}$ = 3.260, p = 0.004; in contrast, frontocentral ROI ($t_{(1,19)}$ = -.676, p = 0.507) (Fig. 4-7).

In addition, we also computed the interaction between hemisphere and memory load for mean amplitudes from those same electrode sites included in the former analyses of stimulus-locked potentials (i.e., vCDA). After subtraction of visual-evoked potentials, in both stimuli conditions repeated-measures ANOVA yielded no significant main effects of hemisphere or load (all Ps > 0.05). Moreover, the interaction between these factors did not reach significance when memorising geometrical shapes (F(1,19) = 0.175, p = 0.680) or hand stimuli (F(1,19) = 0.076 p = 0.786. These latter results confirm that visual activity was certainly subtracted from the concurrent visual and motor activity of the visual-motor trials.

Overall, MCPs modulated by memory load were found in the hand stimulus condition whereas no modulation by load was found in the shape stimulus condition. While activity from the ipsilateral hemisphere did not significantly interact with stimuli, mean amplitudes of the contralateral hemisphere showed a significant interaction between ROI, load, and stimuli types. Here, differential activity between holding in 1 or 2 hand images in WM was found over the frontal electrode sites. In essence, our results suggest that holding in WM body-related stimuli such as hand images involves neural

recruitment of motor regions, which are known to underpin the perceptual representation of body stimuli beyond visual cortices (namely, sensorimotor involvement in WM for visually perceived bodily information).

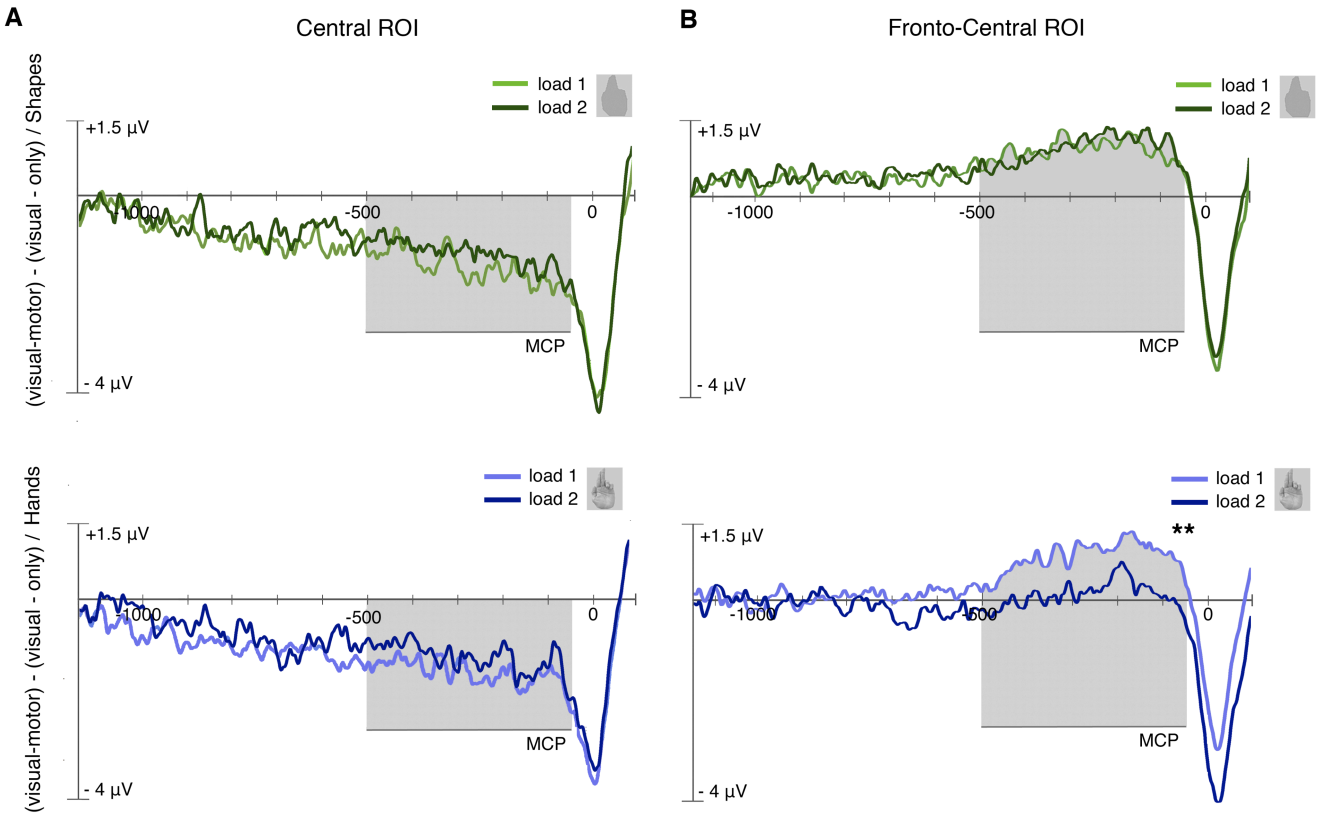


Figure 4-7. Results of response-locked motor-cortical potentials (MCPs) in contralateral waveforms over central and fronto-central ROIs for each memory load and stimuli conditions after subtracting visual activity from visual-only trials. A motor preceding negativity can be observed nearly half second before the actual motor response (0ms). *(A)* In the central ROI no significant differences of mean amplitudes modulated by memory load were found. *(B)* A significant difference of mean amplitudes modulated by memory load was only found in the hand stimulus condition (**) No differences were found in the shape stimulus condition. Grey squares indicate time windows for statistical analyses and further sLORETA estimation. n=20; **, $p < 0.01$; positive ERP plotted upward.

4.4.4 Electrophysiological source localization

Based on the scalp-recorded electric potential distribution, the Standardised Low-Resolution Brain Electromagnetic Tomography (sLORETA) (Pascual-Marqui, 2002) was used to estimate cortical source estimation. It was performed on the MCPs (response-locked potentials, -500 to -50ms) after obtaining the differential brain activity between stimuli types once subtracted the brain activity due to each memory load (i.e., load 2 minus load within stimulus). This identified a set of regions whose peak of activity was maximal for the hands condition *vs.* shapes stimulus condition (Fig. 4-8). Candidate regions where maximum differential activity was due to load differences between stimuli conditions was source localized in classical motor cortical regions, in precentral and superior frontal gyrus (Brodmann areas 6/4), and postcentral gyrus over parietal lobe (BA 3). These include premotor cortex, SMA, primary motor cortex, and primary somatosensory cortex over caudal postcentral regions.

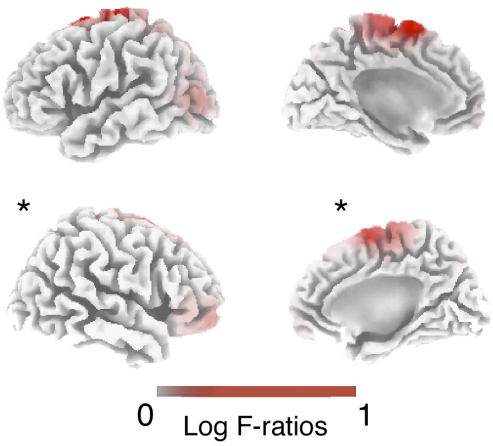


Figure 4-8. Candidate brain areas in MCPs. Three-dimensional representation of sLORETA showing candidate regions with maximal differences due to load differences (i.e., load 2 minus load 1) between stimuli conditions. Candidate regions were found in sensorimotor cortical regions (BA 3, 4, 6).

4.5 Discussion

In the present study we explored the neural recruitment of visual and motor areas during WM for visual information depicting body-related stimuli. We present a novel signature of sensory recruitment during encoding and maintenance of these stimuli (i.e., hand images) beyond those perceptual streams engaged in the original influx of the percept. Such neural activity was found over frontal electrode sites in motor cortices and was elicited by asking participants to synchronously perform a bimanual task-irrelevant response during active maintenance of the stimuli in WM. Furthermore, we developed a novel paradigm based on elicited activity from different neural sources by subtracting evoked activity from visual-only trials to visual-motor trials, allowing us to detect independent neural responses evoked in motor cortices during visual processing, diminishing carryover visual effects from the visual evoked responses. The core of this method relies on combining different evoked-potentials to ultimately isolate a region or process of interest. In our specific case we combined and used two renowned neural signatures (i.e., vCDA and cued version of RP; MCPs). This methodology provided us with motor-cortical potentials from which visual activity spreading from more posterior areas was subtracted. Similar approaches have been taken in the past when studying integration of information from distinct sensory modalities (Talsma et al., 2010; Sel et al., 2014), and during decision-making associated to motor activity and volitional body movements (Alexander et al., 2016).

Moreover, analogous to earlier studies examining visual and somatosensory mechanisms in attention and WM (Vogel and Machizawa, 2004; Katus et al., 2015), we took advantage of the primary contralateral organisation of motor cortices. Since our own hands' cortical representation is well lateralized (Martuzzi et al., 2014) and observing others' actions such as manual acts seem to engage similar areas than

those required in the action itself (Shmuelof and Zohary, 2006; Molenberghs et al., 2012), we postulated that the resemblance between action and perception could underpin mnemonic representation of hand images. Precisely, this is likely the underpinning mechanism found in our interhemispheric difference: a neural trace beyond the input modality in which lateralization is driven by visually perceiving body information, known to engage sensorimotor regions in a lateralized somatotopic manner.

Visual activity from visual-only trials. In congruency with previous studies, the visual-evoked potentials elicited an interhemispheric difference known as contralateral delay activity over visual brain areas (McCollough et al., 2007; Tsubomi et al., 2013; Luria et al., 2016). This delay activation is associated with encoding and active maintenance of visual stimuli such as shapes and colours in WM. Interestingly, visual areas during retention of hand images also exhibited vCDA.

MCPs after subtracting visual activity from visual-only trials. Our experimental manipulations allowed us to observe a clear MCP, extending in a retrospective window from the encoding of the stimuli, through their consolidation in memory, until the actual motor response. Despite such a response being elicited over frontocentral and more clearly over frontal electrode sites in both hemispheres, an interhemispheric interaction modulated by the quantity of stimuli to-be-remembered and the type of stimuli was only found in the contralateral cortex of the attended hemispace. Follow-up tests of this modulation showed that only when participants were remembering images of hands the MCPs were modulated by load (i.e., increasing mean amplitudes with the number of body-related stimuli to be remembered). Such difference was not found when remembering the control visual stimuli (geometrical shapes).

Our findings exhibit novel evidence for neural recruitment in motor cortices during representation of visual information depicting body images in WM. Therefore, the nature of memoranda seemed to interact with sensorimotor cortices beyond visual areas, eliciting activity in cortices matching the sensory associations of the functional and perceptual encoding features of the perceived stimuli.

4.5.1 Stimuli-specific and additionally driven neural signatures

After perceiving sensorimotor information, the initial input seems to be rapidly driven onto body-related and associative brain areas, reaching a closer representation of our own body and effectors of the action in the brain, including premotor, parietal, and occipitotemporal cortical regions of the human brain (Caspers et al., 2010; Grosbras et al., 2012). Crucially, our data suggest that motor cortices possess a further role in encoding and maintaining *visual* body information. In congruency with our results, current accounts in WM postulate that temporary representation of stimuli befalls in brain areas such as sensory cortices (D'Esposito, 2007; Harrison and Tong, 2009; Tsubomi et al., 2013). These representations would arise by activating one of the several states of the information that have been built through perceptual experience and continuing sensory associations. The results from the current study contribute to this formulation by suggesting that visual information is not only re-established by those brain regions involved in the initial sensory stream, but also by those 'functionally built' by previous sensory cortices. Interestingly a WM system dealing with sensorimotor components conveyed in body-related information has been suggested. Smyth and colleagues (1988, 1989, 1990) showed that observing another person's body movements disrupts WM for body configurations. Moreover, in another study with a behavioural procedure comparable to ours, remembering body postures and simultaneously being asked for visual and spatial information of objects did not interfere with recalling the visually displayed body postures (Wood, 2007).

Similar to the present study, stimuli driven activity has been reported. Previous studies have described neural recruitment contingent to the specific characteristic to-be-remembered within a given stimulus (Serences et al., 2009; Lee et al., 2013), as well as the type of stimulus included in the WM task. Fusiform face area and parahippocampal place area, known to particularly respond to encoding of faces and scenes, support memory associations between pairs of faces and buildings and specific memory maintenance within these categories (Ranganath et al., 2004). Other studies also found that fusiform face area and a further distributed network of brain regions including more frontal substrates are recruited during WM for faces (Gazzaley et al., 2004).

A more recent study suggests that WM for real objects is greater than for non-real objects. Greater performance and encompassing CDA were found when holding in memory real objects (yet, this higher CDA seemed to vary depending on the memory load) (Brady et al., 2016). In the present study, we created control stimuli in form of analogous versions of the body-related stimuli and participants had similar behavioural performance in both stimuli conditions. Here, it is possible that perceptual differences could partially explain our results. However, as Brady et al. (2016) discussed, previous studies in long-term memory have already highlighted how the nature of the information embedded in the memoranda seems to play a key role beyond perceptual complexity (McWeeny et al., 1987; Konkle and Brady, 2010).

Our dissociation of scalp potentials by the use of a task irrelevant motor task, the only purpose of which was to elicit an observable cortical response over sensorimotor cortex during encoding of visual information, is coherent to the distinctive conceptual information conveyed in our body and non-body-related visual memoranda. In the same vein, holding in WM manipulable objects has shown neural recruitment of motor brain areas that closely overlap those required for their actual

manual manipulation (Mecklinger et al., 2002, 2004). Nevertheless, we expand this work by adapting a well-known paradigm in WM with higher temporal resolution while developing a novel manipulation that suggests involvement of body-related cortices to hold body-related information (beyond motor affordances in memory for objects).

4.5.2 Interhemispheric effects in cognition

While the current study suggests novel evidence of sensory recruitment beyond input modality, it also opens a wide range of inquiries that require further work. One of the relevant remaining questions concerns the very specific content of the load effects over sensorimotor cortex. Sensorimotor cortices represent motor-related content and actions that are visually perceived, resembling activity elicited when actually moving our own body. For instance, seeing the characteristics conveyed in different actions elicits brain activity from which specific motor-content can be reliably decoded from motor-related brain areas such as premotor cortices (Wurm and Lingnau, 2015; Wurm et al., 2016). As reviewed by Man et al. (2013) fMRI studies decoding actions from motor and sensory systems expose shared representations in some of the dimensions between perceptual mechanisms of action observation and motor execution. Assuming the main postulate of sensory recruitment models (i.e., WM underpinned by perceptual brain areas), it is feasible to recognize that similar mechanisms support mnemonic processes link to body-related information.

A second issue to be explored concerns the particular role of ipsilateral and contralateral motor cortices in memory. MCPs and magnetic field cortical-potentials show that even unilateral manual responses elicit neural activity associated to motor preparation over ipsilateral and contralateral hemispheres (Kristeva et al., 1991; Erdler et al., 2000). Functional connectivity supports both motor cortices through mechanisms of interhemispheric inhibition and facilitation that together with interactions of local intracortical circuits shape motor cortical output (Reis et al.,

2008). Based on standard procedures, our contralateral and ipsilateral waveforms are based on mean amplitudes across participants attending to either the right or left hemifield; including right and left hand images, respectively. We assumed that our averaged waveforms reflect a linear lateralization driven by visually perceiving body information, known to engage sensorimotor regions in a contralateral and somatotopic manner. Nevertheless, contralateral/ipsilateral MCPs' amplitudes could vary depending on the laterality of the hand images conveyed in the array to be attended/ignored (i.e., left and right hands). Note that here we are strictly referring to the effect that lateralized body images (left/right limbs and body parts) have on driving lateralized brain activity.

A third issue to be explored concerns potential 'simon effects' (i.e., faster and more accurate responses when stimuli are presented in the same location as the responses, even if these are irrelevant to the task). From a S-R compatibility framework, it is possible that our stimuli, which were presented in a lateralized manner (i.e., left and right hemifields), could have prompted participants in their task-irrelevant motor responses or even in their verbal responses during the upcoming memory task. Encoding hand images at the beginning of the trials and having to wait to exert a motor response 800ms later could have recruited additional resources just to refrain from initiating an earlier/prompted motor response. Nevertheless, MCPs seem to arise after response selection (being affected by S-R compatibility effects) but before motor programming (being affected by response complexity) (Praamstra, 2007; Smulders and Miller, 2012). Note that we kept constant the timing of the cue indicating when to press (lowering expectancy effects), the motor response was kept as simple as possible (mere key pressing), the motor response itself was task-irrelevant (no extra cognitive load), and that other non-specific bilateral contributions

(e.g., attentional shifts) were assumed to be deducted by the subtraction of mean amplitudes from visual-only trials.

Our study was not designed to shed light on the –intra and –inter hemispheric effects, nor on the specific direction of the increasing interhemispheric differences between load and stimuli conditions, but to show effects that resemble perceptual processing of body-related information during memory consolidation for bodily percepts to-be-remembered. Overall, hypotheses on mnemonic content are difficult to tease apart within the context of the present study. Further studies may untangle mnemonic content and sensorimotor processing during WM for body-related images by studying lateralization of MCPs during encoding of lateralized-body images.

4.5.3 Conclusions

In conclusion, we combined pieces of evidence from different research fields to create a novel paradigm using the readiness potential as probe of motor processing in a visual WM task. Readiness potential is associated with the lateralized motor representation of the body part used to execute a given movement, and it is modulated by complexity of the performed, imagined, and observed actions (Eimer and Coles, 2003; Kilner et al., 2004; Masaki et al., 2004; Kranczioch et al., 2009).

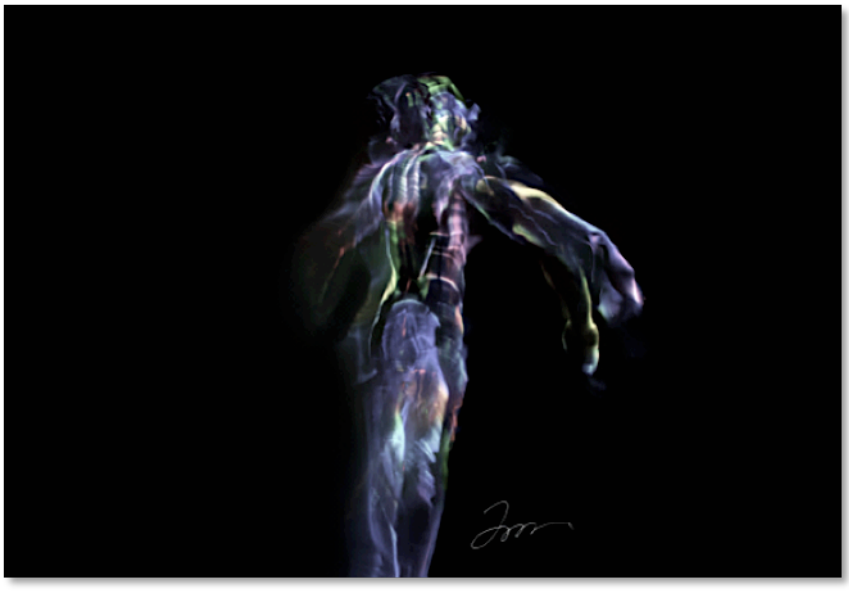
Our findings show how the sensory channel to 'acquire' the information does not necessarily dictate the active maintenance of stimuli to-be-remembered. This maintenance seems also contingent to those functional associations underpinning the neural representation of the percept in WM. We provide original evidence for a novel principle of WM processing, which is grounded on the relevance of previous motor and sensory associations as precursor of persistent neural activity link to WM. While previous studies have shown that visual information similar to our control condition stimuli is represented in posterior and visual cortices (Todd and Marois, 2004; Vogel and Machizawa, 2004; McCollough et al., 2007; Tsubomi et al., 2013)

and tactile information in somatosensory cortices (Harris et al., 2002; Katus et al., 2014) our results support a more dynamic process, in which the memoranda can be represented beyond sensory-input cortices. Thus, information-representation is not forcefully constrained in a limited number of highly specialised memory systems (Postle, 2006; D'Esposito and Postle, 2015). This sort of efficient model of information-representation is now becoming prominent in WM research whereas in the action observation field it has been well established in the study of the equivalence between perception and motor execution.

4.6 Special section: Artistic impressions III

Bodily Realm – Tactile or motor? (2015) Photography on board (30 x 45cm) / AGP

Holding bodily images in one's memory implies sensorimotor resonance in the brain. Bodily-visual information is shared across cortical regions, beyond the visual and the first of the stops in bodily matters, the sense of touch, motoric regions seem to be involved too.



Bodily Realm – Multidimensional bodies (2015) Photography on board (30 x 45cm) / AGP

Our own body is a kaleidoscopic representation. Multiple representations of the body co-exist, dimensions and layers, echoing, mirroring and changing over time.

5. Chapter 5: Disrupting sensorimotor processing during WM for body and non-body-related images.

5.1. Introduction

Previous studies have suggested the presence of a WM system contributing to memory encoding of visually perceived body information (e.g., Smyth el al., 1988; Moreau 2013). In the previous chapters I investigated two brain regions that could underpin such system: (1) in the first EEG study - *Chapter 3,* I examined brain activity arising from somatosensory cortex during a WM task where stimuli to-be-remembered were body and non-body-related images. (2) In the second EEG study – *Chapter 4*, I developed a version of the latter paradigm that allowed us to examine activity arising from motor cortex. Our results showed that the number of body images to be held in WM (i.e., memory load) modulates contralateral somatosensory and motor cortices. Conversely, this interaction did not appear when encoding control non body-related images.

Nevertheless, the enhancement of EEG waveforms reported in the previous studies does not indicate whether or not such activity is directly linked to an effective encoding of the stimuli in WM. The EEG studies were not designed to investigate the causative role of the sensorimotor complex during WM. For these reasons, in the current chapter we adapted the behavioural paradigm used in the previous studies to create three experiments. These experiments incorporate a dual task that is concomitant to the encoding and maintenance of the stimuli in WM. The purpose of the dual task is the disruption of sensorimotor processing. Then, if sensorimotor

cortices as responsible for the factual encoding of visually perceived body information, memory performance may be affected by exhaustion of mnemonic resources.

In the following chapter I outline behavioural studies that have used dual tasks (also known as concurrent, secondary, or suppression tasks) to interrupt WM maintenance of bodies and actions. Then, I will introduce how suppression tasks can be used to interrupt and/or overload the processing of those areas investigated in the previous EEG studies. Third, I will introduce the overall hypotheses of the study, methodological aspects, and considerations. Importantly, the specific goal, context, and results of the three experiments are presented separately in the corresponding sections. Finally, I will discuss the main findings of the three experiments

5.1.1. Delineating systems: use of interference in processing of body-related information

A well-known method to inspect the role of a memory system is the insertion of an experimental manipulation that alters its regular functioning. This can be accomplished by asking participants to perform a task (i.e., a secondary task) during the encoding, maintenance, and/or retrieval of the stimuli to-be-remembered (i.e., primary memory task). Researchers have used secondary tasks to interrupt and interfere with memory systems by exploiting their limited capacity and their rather specialised processing of information; the principle behind this approach is based on the limited capacity of any cognitive system. If a given system is both limited in capacity and dedicated to a particular type of information (*A* but not *B*), it is possible to disrupt its course by asking a participant to process additional *A.* Contrary to this, asking someone to process or carry-on a *B-r*elated task should not interfere dramatically with the corresponding memory processing. Therefore, much like investigating patients with specific impairments or brain damage, manipulations that

exhaust cognitive resources in typical populations help to delineate and investigate the workings of the brain. Disentangling and targeting specific memory processing is challenging, as several types of information are normally embedded in a single percept and each type is potentially processed across different systems. Behavioural studies that manipulate the course of memory encoding and consolidation usually need to include several manipulations and experiments in the same paper.

Studies using behavioural interferences to interrupt memory encoding of visually acquired body-related information are scarce. To our knowledge there are approximately a dozen. In the present chapter, *table 5-1* lists the studies that have used interference tasks to provide evidence of a WM system for visually perceived body-related information. The studies in the table normally include presentation of stimuli in serial order, memory tested through visual recognition or action execution, and different types of interferences such as articulatory and spatial.

One of the first things to note on the table is the larger number of studies that have tested memory recall by using visual recognition compared to action execution. However, the results lead to similar conclusions: separation between memory systems for spatial, verbal, visual, and body-related stimuli. For instance, Smyth and colleagues (1988, 1989) showed a double dissociation between the number of body movements to-be-remembered (i.e., hand movements) and another task involving hand movements to specific spatial locations. Specifically, participants were asked to reproduce an increasing number of hand configurations while performing two different concurrent tasks (movement and spatial). The results showed that memory span for hand movements was significantly impaired by alternating the opening and closing of the hand, but not by the pointing with the hand to different locations. In another experiment, spatial memory was tested using the Corsi block task while participants

were newly asked to perform a movement or a spatial suppression task. Performance in the Corsi block was significantly affected only by the spatial suppression task.

The double dissociation shown in the results of Smyth et al. (1988, 1989) suggests the presence of a WM system dedicated to maintaining body-related information, which can be dissociated from a more specialised system for spatial information about locations in space. Interestingly, the sensorimotor interference of the motor suppression seem rather independent on the body part involved in both suppression and further recall. The number of correctly remembered hand configurations decreased when motor suppression involved in moving the left or right hand during encoding of right hand movements (Smyth and Pendleton, 1989).

In a similar vein, Woodin and Heil (1996) asked participants to remember a set of numbers in their relative spatial locations within a matrix (Brooks, 1967) as well as body configurations adapted from Smyth et al. (1988). Here, a square tapping task and tapping of the body were used as suppression tasks for spatial and body processing, respectively. Results showed that memory span for spatial locations in the Brooks task were worse when accompanied by square tapping whereas span for body configurations diminished when concomitant to body tapping.

Interestingly, encoding body-related stimuli seems to interfere with movements and actions that do not require a memory component. In a second experiment, Woodin and Heil (1996) tested participants' memory in the Brooks task and for the Smyth studies' body configurations. Interestingly, participants were rowing while encoding those tasks. Rowing involves two continuous movements: spatial movements of the oar to 'catch' the water and a reposition of the body configuration to close the driving phase and prepare for the following catch (hands away movement). The results showed that encoding the Brooks tasks made worse the timing of the participants' catch but not the hands away movement whereas the inverse outcome was found

when asked to remember body configurations. These results indicate that different stages of a continuous movement alternating between processing of spatial and body configurations can be specifically affected by memory tasks demanding spatial and more body-centred computations.

5.1.1.1. Perception of bodies and actions interferes WM for actions

Smyth et al. (1990) showed that just observing another person's body movements while holding in memory body configurations decreased memory span. In three different experiments they showed that after a short interval, recall of body configurations is affected by watching similar movements during the interval, as well as by reproducing similar movements, and encoding another set of movements during the interval. Conversely, making or observing movements to spatial locations, as well as articulatory suppression did not interfere to the same extent with memory span for body configurations.

Moreover, a delay match paradigm adaptation from studies in WM for arbitrary stimuli such as coloured squares and lines (e.g., Luck and Vogel, 1997) showed that responding to differences between computerized displays of body postures and actions, and also being asked to hold in memory visual and spatial objects does not interfere with recalling bodily actions (Wood 2007) (Wood experiments 4-8, see table 5-1). Conversely, sensorimotor memory, here specifically related to observed actions, is affected by remembering other types of non-body-related information when both stimuli set possess some degree of sequential information. Then, holding in memory changes in non-body stimuli that occur within a continuous presentation and a determined space interferes with holding in memory body stimuli that have been presented under similar characteristics (Smyth and Pendleton, 1990; Woodin and Heil, 1996; Wood 2007; Vicary et al., 2014).

Study	Exp no.	Task	Main experimental manipulations	Body stimuli to-be-remembered	Non-body stimuli to-be-remembered	Recall for body stimuli	Main findings
Smyth et al. (1988)	Exp. 1	Serial encoding of body movements and words (similar in *Exp. 1* and *2*)	Presence of articulatory suppression	Bending, crossing, and straighting limbs (similar in all experiments)	Words	By action execution (similar in all experiments)	Articulatory suppression decreased recall of both body and non-body stimuli
	Exp. 2		Presence of motor suppression		Words		Motor suppression decreased recall of body movements but not of words
	Exp. 3	Serial encoding of body movements and spatial locations	Presence of motor or articulatory suppression		Spatial locations (Corsi Block)		Articulatory and motor suppression but not spatial decreased recall for body movements. Motor suppression did not affect spatial recall.
	Exp. 4	Serial encoding of familiar movements	Presence of motor or articulatory suppression		NA		Familiarity decreases the effect of articulatory suppression. Memory for body movements was similar.
	Exp. 5	Serial encoding of familiar movements	Presence of spatial suppression		Spatial locations (Corsi Block)		Recall of body movements did not affect spatial suppression, which impacted recall of spatial locations
Smyth and Pendle-ton (1989)	Exp. 1	Serial encoding of hand movements	Presence of motor or spatial suppression with left or right hand	Configurations of the right hand (finger positions / hand postures)	NA	By action execution (similar in all experiments)	Regardless laterality of interference, the motor but not the spatial suppression decreased memory span for hand movements
	Exp. 2	Serial encoding of spatial locations	Presence of spatial suppression with left or right hand	NA	Spatial locations (Corsi Block)	By pointing locations with right hand	Regardless laterality of interference, spatial suppression decreased memory span for spatial locations *Further analyses:* combining data from *Exp. 1* and *2* shows that suppression tasks are slower when paired with matching memory tasks.
Smyth and Pendle-ton (1990)	Exp. 1	Serial encoding of body movements (similar from *Exp. 1* to *3)*	Recall after immediate, delayed, or filled delay with articulatory, motor, or spatial task.	Bending, crossing, straighting limbs (similar to Smyth et al., 1988 and similar from *Exp. 1* to *3*)	NA	By action execution	Merely copying other's actions during retention of body movements disrupts memory for movements.
	Exp. 2		Recall after filled delay with watching other's actions / 1 vs. 2 sets of movements to-be-remembered		Spatial locations (Corsi Block)	By pointing locations with right hand	Just observing other's actions decreases memory span for body movements / Holding a second set of body movements impairs memory / Spatial-filler task impacted in a lesser degree memory for body movements.
	Exp. 3		As above but recall of body movements with no order (free recall)		As above	As above	Similar to *Exp .1* and *2,* only watching or having to recall higher span of body affects memory span for movements. Average immediate-free recall: 4 movements.

	Exp. 4	Encoding locations in space	Immediate recall, delayed, or filled delay with observation of motor or spatial task.		Spatial locations (Corsi Block)	By pointing locations with right hand	Serial recall was affected by watching the pointing of locations during the filler task. Watching body movements did not affect this. *Overall results:* just watching and doing similar movements during retention of movements affects recall of body movements (in free and serial recall). Less interference is found when intervening tasks are word or spatially related.
Quinn and Ralston (1986)	Exp. 1	Encoding locations in space as exe-cuting movements (similar all *Exp*)	In/compatible arm movements during encoding locations to-be-remembered	NA	Spatial locations (Brooks task) (similar in all *Exp.*)	NA	Incompatible movements affected memory for spatial locations.
	Exp. 2		Same as above but manipulating degree of familiarity with the tasks	NA		NA	Regardless of familiarity and subsequent allocation of attention, incompatible movements affected memory for spatial locations
	Exp. 3		In/compatible movements were performed passively (arm being moved) or actively	NA		NA	Performing both active an passive arm movements while encoding locations in space led to poorer recall of locations in space
Woodin and Heil (1996)	Exp. 1	Serial encoding of body movements and spatial locations (fairly similar in both *Exp. 1* and *2*)	Presence square tapping or body tapping during encoding of stimuli to-be-remembered	Meaningless actions: bending, crossing, straighting limbs (adapt. from Smyth et al., 1988 and similar in *Exp. 1-2*)	Brooks task (in both Exp.)	By action execution (similar in both Exp.)	Similar to Smyth et al. (1988, 1989). Double dissociation between type of suppression and memory: square tapping affected memory for locations and body tapping affecting only memory span for body movements.
	Exp. 2		Rowing while encoding stimuli to-be-remembered				Selective impairment in continuous rowing movement ('catch water' timing affected by encoding locations and patterned body posture 'hands away' disrupted by encoding body movements.
Rumiati and Tessari (2002)	Exp. 1	Serial encoding of actions (similar in *Exp. 1* to *3*)	Presence of motor suppression and degree of familiarity with actions to-be-remembered	Meaningful actions (pantomimes of objects use) and meaningless actions (modified pantomimes)	NA	By action execution (similar in *Exp. 1* to *3*)	Memory span for meaningful actions is better than memory for meaningless actions
	Exp. 2		Presence of articulatory suppression concomitant to motor suppression or spatial suppression	Same as above	NA		Articulatory + motor suppression affects more memory span for actions than articulatory-only and articulatory + spatial suppression
	Exp. 3		Only articulatory, motor, or spatial suppression (i.e., no simultaneous)	Same as above	NA		Motor suppression affects more memory span for actions than spatial suppression
	Exp. 4	Encoding of object pantomimes	Presence of articulatory, motor and spatial suppression	Words related to object pantomimes	NA		Similar word recalling after suppressions. Motor and spatial suppressions required similar resources (e.g., effects not due to distinct difficulties in suppression tasks)

Wood (2007)	Exp. 1	Serial encoding of actions in delay-match paradigm (similar in *Exp. 1-4*)	Only the increasing number of actions	Avatar displaying full body-meaningless actions (similar in all *Exp.)*	NA	Visual recognition in a detection change (delayed match) (similar in all *Exp.)*	Only 2.5 actions are remembered. WM capacity highly limited.
	Exp. 2		Duration of encoding (short and long display)		NA		As above, only 2.5 actions remembered independently of the time of encoding (500ms *vs.* 750ms displays)
	Exp. 3		Participants asked to also remember type and duration of actions		NA		Memory capacity is similar for different types of action properties
	Exp. 4		Participants asked to also remember type, duration, and laterality of actions		NA		Integrated representations of actions: It is possible to remember 9 properties distributed across 3 actions as well as 3 properties distributed across 3 actions.
	Exp. 5	Serial encoding of actions and objects in a delayed-match paradigm	Participants asked to remember 0 to 3 actions as well as 0 to 6 other non-body stimuli. Recalled to both		Coloured squares (all presented at once)		Equal memory for actions regardless number of non-body-related stimuli maintained in WM / Diff. systems of WM (for observed actions and objects)
	Exp. 6	As above	As above, but participants only recalled one stimulus type at the end of the trial		As above		Similar results to *Exp. 5*
	Exp. 7	Serial encoding of actions and spatial locations in a delayed-match paradigm	As above but participants had to recall actions or spatial locations (0 to 6 locations)		Locations in a grid		Similar results to *Exp. 5* and *6* / Diff. systems of WM (for observed actions and spatial locations)
	Exp. 8	Serial encoding of actions and objects in a delayed-match paradigm	Similar to *Exp. 5* and *6*.		Coloured squares in serial order (as the body stimuli)		Memory span for serial actions affected by concomitant encoding of serial non-body-related information. Some WM processes are shared when encoding serial information.
Wood (2008)	Exp. 1	Serial encoding of actions and agents in a delayed-match paradigm (similar in all *Exp*).	Participants asked to remember either actions or agents' actions, or both (similar in all *Exp*).	Avatar displaying full body-meaningless actions (similar in all *Exp.)*	Agents of actions: avatars with diff coloured clothing)	Visual recognition in a detection change (delayed match) (similar in all *Exp.)*	Maintaining both agents and actions in WM consumes resources associated with binding. Agents and actions seemed to be stored in different WM systems
	Exp. 2				Agents displayed in non-overlapping spatial locations		In *either* or *binding* conditions, memory performance reflected performance of the WM system with lowest capacity /
	Exp. 3				Agents were presented with a 50ms gap		Similar to *Exp.1* and *2*
	Exp. 4	As above	As above	As above	Agent differed in colour/type of clothing, gender, age, and facial features	As above	Similar to *Exp.1* to *3*
							Overall conclusions Exp 1 to *3:* binding actions and agents requires binding features from different memory stores. Visual cues aid this process

Cortese and Rossi-Artnaud (2010)	Exp. 1	Serial encoding of ballet movements	Presence of spatial suppression (finger tapping)	Ballet movements were listened and not visually presented.		By action execution (similar in all experiments)	Spatial suppression did not interfere with memory span for ballet movements (Approx. 3.6 movements regardless suppression)
	Exp. 2	Serial encoding of ballet movements in specific spatial locations	Presence of spatial or motor suppression	As above	Concurrent to ballet move-ments, locations visually diplayed	Ballet movements performed in specific locations on stage	Motor suppression increased errors on recalling ballet movements when these are coupled with spatial locations.
	Exp. 3	Serial encoding of locations in space	Same as above	NA	Locations in space (crosses across stage)	Walking to locations on stage	Only spatial suppression increased the number of errors when recalling spatial locations
	Exp. 4	Serial encoding of ballet movements	Similarity between ballet movements (list of similar *vs.* list of dissimilar movements)	As *Exp. 1* and *2*	NA	By action execution	More errors when ballet movements to-be-remembered were more similar. Equivalent to memory studies using words, similarity plays a role in WM for patterned movements
Moreau (2013)	Exp. 1	Serial encoding of body postures	Expert and non-expert participants. Presence of verbal and motor suppression.	Full body stimuli displaying movement of arms and legs.	NA	By recognition of body movements (ordered) in a visual display showing all stimuli	Body experts did better during *non-suppression* and *verbal suppression* conditions. The latter affected more the non-experts. Conversely, motor suppression affected more the experts.
Vicary et al. (2014)	Exp. 1	Serial encoding of dance-like actions in a delayed-match paradigm (similar in both *Exp.*)	Encoding dynamic actions or snapshots of these actions / being tested for snapshots or dynamic stimuli	Dance-like actions from Calvo-Merino et al. (2005)	NA	Visual recognition in a detection change (delayed match) (similar in both *Exp.*)	Congruency effects between encoding and test form: Greater performance for dynamic movements when preceded by encoding of dynamic stimuli and *vice versa*.
	Exp. 2		Encoding static or dynamic actions and presence of static or dynamic spatial suppression	As above	Spatial loc (Corsi Block) displayed at once(static) or sequentially(dynamic)		Recognition of dynamic stimuli was impaired by dynamic but not by static spatial suppre-ssion. However, no effect of suppressions were found when encoding static actions
Shen et al. (2014)	Exp. 1	Encoding of biological motion	Only the increasing number of actions	Points of light displaying actions. 1 to 5 actions showed at once (similar in all *Exp.*)	NA	Visual recognition in a detection change (delayed match) (similar in all *Exp.*)	Only two to three actions can be retained. With longer encoding performance increased by one more action.
	Exp. 2	Encoding of biological motion and colours	Task requirements: encoding of stimuli displaying biological motion, non-biological motion, or both (Similar in *Exp* 2 to 5)		Coloured figures		Doing both memory tasks (for biological motion and coloured stimuli) does not affect memory performance. Independency of systems.
	Exp. 3	Encoding of biological motion and spatial loca-tions					Memory for biological motion and spatial locations did not mutually affect each other.
	Exp. 4	Encoding of biological motion and shapes			Geometrical shapes		Memory for biological motion and shapes did not mutually affect each other.
	Exp. 5	Encoding of biological and non-biological motion			Circled stimuli, rotating and moving		Memory for biological motion is affected by maintaining non-biological motion.

5.2. Aims, methodological approach, and predictions Exp 1 to 3

5.2.1. Concatenating concepts

In the present study there are five points that need to be considered 1) behavioural studies indicate that a similar cognitive system underpins perception, execution, and memory for bodies and actions (table 5-1). 2) In *Chapter 3* and *4,* we showed that two of the neural candidates to support such processes, somatosensory and motor cortices, exhibit brain amplitudes that increase together with the number of body images to-be-remembered. 3) Nevertheless, the modulation of brain amplitudes *per se* does not convey whether or not those brain regions support the effective/causative encoding of visually perceived body stimuli in WM. 4) Therefore, we decided to interrupt the likely sensorimotor processing of body images by adding a secondary task (i.e., moving one's hand/s) that was performed in three different versions across three different experiments. The only purpose of the secondary task was to interrupt/overload sensorimotor processing through exhaustion of computational resources that could be otherwise allocated to the primary memory task.

Aims of the study. While our EEG studies showed contralateral involvement during encoding and maintenance of hand images in WM, earlier studies from Smyth and colleagues indicated a more general involvement where either hemisphere (contralateral and ipsilateral) seems to participate in such processes. Here, we aim to shed light on these, at first sight, contradictory observations. Specifically, the present study sought to answer two complementary questions; the first one refers to whether or not contralateral sensorimotor areas, which showed enhancement of activity during encoding and maintenance in *Study 1* and *2,* support memory maintenance of the stimuli in WM (i.e., is memory performance for visual stimuli depicting right hand postures disrupted by a sensorimotor interference performed with the right hand?). The second question concerns the overall involvement of such cortical areas: the question

of whether or not sensorimotor cortex plays a role in WM for body-related visual information as a general system (i.e., regardless contralaterality; is memory performance for visual stimuli depicting hand postures disrupted by a sensorimotor interference performed with either hand?).

Methodological approach. We adapted the previous two EEG studies, creating three different behavioural versions of the same visual WM paradigm. In the first two experiments participants had to remember different left or right hand postures while performing a unimanual motor suppression with their left or right hand. In the third experiment, this latter motor suppression was bimanual and the key factor was its presence or absence. In addition to the behavioural analyses computed in the previous studies (i.e., sensitivity index *d'*) the proportion of hits and false alarms, the index of bias *C,* as well as reaction times were analysed.

The main factors in Experiment 1 were as follow: memory load (1, 2, 3 images), congruency of the unimanual suppression task (congruent: e.g., participants' left hand movement while encoding left hand images; incongruent: participants' left hand movement while encoding right hand images). In experiment 2: memory load (1, 2, 3 images), stimulus type (shape, hand images), congruency (incongruent, congruent suppression). In Experiment 3: memory load (1, 2, 3 images), stimulus type (shape, hand images), bimanual suppression task (present, absent). Remarkably, the inclusion of memory load 3 in the current experiments may allow exploring effects of memory load that our previous and more extended EEG experiments did not incorporate. We did not include memory load 3 in the previous electrophysiological studies because this would have involved more than 4.5 hours of testing by participant (in one single session), which seems utterly fatiguing and compromising for the results.

Predictions. We predicted that WM performance for body-related information would be disrupted by the motor suppression whereas memory for non-body-related stimuli

would not be affected by such suppression. More specifically, we predicted that motor suppression would interact with increasing memory load of body stimuli to-be-remembered. Conversely, no interaction is expected when holding in memory non-body stimuli. With these designs and methodology, we sought to modulate participants' performance by actively engaging their sensorimotor system in a dual task that may exhaust resources allocated to sensorimotor WM.

5.2.2. Experiment 1

In *Experiment 1* I asked whether or not contralateral sensorimotor cortices play a specific and causal role in the effective encoding and maintenance of body-related information. To answer this, a unimanual motor suppression used in Smyth and Pendleton (1989) was adapted to the current WM paradigm.

Specifically for this first experiment, on each trial, participants performed a delay-match paradigm between arrays consisting of 1 to 3 different hand images, each displaying distinct hand postures. In a *congruent* condition participants had to remember right hands while constantly squeezing a stress-ball with the right hand and *vice versa*. In the incongruent condition they had to remember right hands while doing the same with the left hand (and *vice versa).*

5.2.2.1. Methods

Participants

Ten participants (6 females; mean age = 25) with normal or corrected-to-normal vision took part and gave informed consent for this experiment, approved by City, University London Psychology Department's Research Ethics Committee. The sample size was chosen based on related studies and paradigm (Wood, 2007, 2008).

Stimuli

The stimuli used in the current behavioural experiments were the same as those used in the first pilot study and the two later EEG studies. A set of 12 pictures containing 6 right and 6 left hands depicting different postures/finger positions were used.

Experimental design, and procedure

The paradigm was similar to those used in the previous studies of this PhD work, except for the insertion of the secondary task. Specifically, participants were seated in front of a LCD monitor (75 Hz) in a dimly lit, electromagnetically shielded room. The forearms of the participants were placed on the top of a table with their hands separated approximately by 25cm, in palm up position and covered by a black opaque surface. Participants performed only one stimulus condition (hand images). They were asked to recall differences between pairs of arrays depicting different hand postures. In each trial a central arrow cue (200ms) instructed the participants to covertly attend to the items in either the left or the right hemifield. After the offset of the arrow cue (300-400ms), the memory array was displayed for 100ms and followed by a blank retention interval of 900ms (Fig. 5-1). As in the preceding studies and in order to avoid potential confounding of sensorimotor encoding of the stimuli in WM with motor responses in the recall, participants responded verbally whether or not the memory and test array were similar or different (P = 0.5). Participants responded *'yes'* if the stimuli were the same or *'no'* if the stimuli were different, these answers were entered by the experimenter, who listened to the participant throughout a speaker/output connected to a microphone placed inside the faraday cage.

Shapes stimuli were displayed using E-Prime Software (Psychology Software Tools). All stimulus arrays were presented within two 4.5° x 8.5° rectangular regions that were centred 4° to the left and right of a central fixation cross on a light grey background. Each memory array consisted of 1, 2, or 3 hands (1.3° x 0.8°) in each hemifield, each

hand being randomly selected from the stimulus set. Right hands were shown on the right hemifield while left hands were displayed on the left. The positions of all stimuli were randomized on each trial with the restriction that the distance between stimuli within a hemifield was maintained to a minimum of 2.4° (centre to centre).

Importantly, we counterbalanced the laterality of the hand involved in the motor interference. At the beginning of each block, participants were instructed to squeeze a stress ball with either their left or right hand at a constant pace and during the whole block; participants only stopped during the breaks (2 breaks in a 20 minutes task). In half of the trials the movement of the hand was congruent to the laterality of the hands to-be-remembered (moving left/right hand while encoding left/right hands, respectively) while in the other half of trials the movement was incongruent (moving left/right hand while encoding right/left hands, respectively) (Fig. 5-1). The resulting paradigm had a total of 252 trials, this is equal to 84 trials for each memory load (1, 2, and 3), half comprising the task-irrelevant sensorimotor suppression in congruency with the laterality of the stimuli to-be-remembered (congruent condition) and the other half with the incongruent matching between the moving hand and those hands to-be-remembered (incongruent condition).

5.2.2.2. Data pre-processing and analysis

Participants' sensitivity. In the earlier studies of this thesis the index of sensitivity *d'* was calculated for each memory load. The overall aim of those analyses was to show that hand and shape images conditions had an overall similar difficulty and that differences in ERPs were not reflecting differences in difficulty. This similarity was accomplished in several steps during the matching process described in *chapter 2.5.* Given that the aim of the current behavioural studies is to investigate effects of sensorimotor suppression over participants' memory performance, it is important to examine not only the final sensitivity index *d'* (i.e., sensitivity to distinguish signal from noise) but also to

investigate how the components leading to its result are modulated. Therefore, in the current behavioural experiments I also analysed the specific hit rates and false alarms.

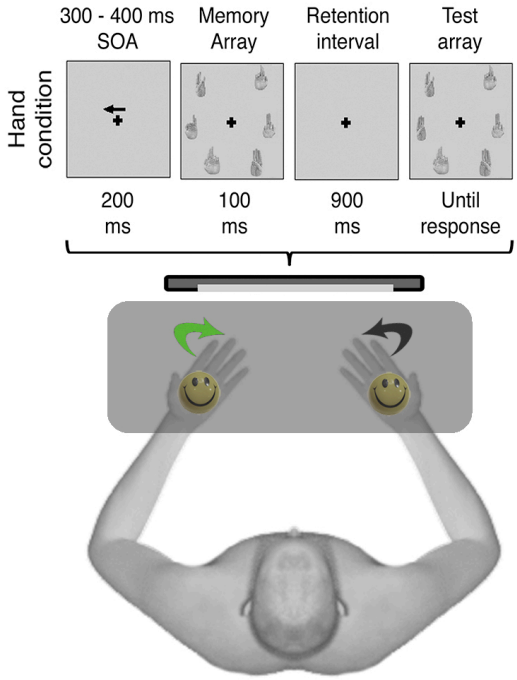


Figure 5.1. Task design and procedure Exp1. In 50% of the trials participants encoded left hand images while squeezing a stress ball with their left hand and *vice versa* (congruent trials) while in the other 50% they encoded left hand images while using their right hand and *vice versa* (incongruent trials). Participants responded verbally whether or not the memory and test array were the same or different (P = 0.5). Here the figure depicts a *'different congruent trial - load 3'* in which hands to-be-remembered are shown in the left hemifield.

As a reminder, *d'* measures the distance between signal and noise means in standard deviation units. The value 0 indicates failure to distinguish signal from noise, in other words, to distinguish old stimuli from new/different stimuli, whereas higher *d'* values indicate increasing capacity to distinguish these. Negative *d'* values are generally due to sampling error or confusion with the response. *d'* is calculated by computing the difference between hit rates and false alarms. In the context of the current experiments this means: calculating the proportion of trials out of the total number of 'same trials' in

which participants correctly state similarity between memory and test arrays, and calculating the proportion of trials out of the total number of 'different trials' in which participants wrongly state similarity between memory and test arrays (i.e., false alarms). Then, both proportions are subjected to the inverse of the normal cumulative distribution that is specified by the mean and standard deviation [$d' = Z(H) - Z(F)$] (the hit and false-alarm rates are named H and F, respectively.)

In addition to the hit rates, false alarms, and the corresponding *d'*, in the next 3 experiments I have also calculated the index of bias c. This parameter measures the distance between the criterion of responses and the neutral point where no response is preferred. This neutral point refers to the specific point where the distribution of signal and noise do actually meet. Positive values of *C* generally indicate participants' bias to respond 'no' whereas negative values indicate bias towards responding *'yes'*, meaning by latter that memory and test stimuli are similar. *C* can be calculated by adding the proportion of hit rates to that of false alarms after inverse normalisation and by multiplying this result by '-0.5'.

Moreover, in comparison to the earlier studies, the next three behavioural experiments include memory load 3 and different forms of sensorimotor suppression (dual task). It is expected that participants' capacity to hold in memory 3 items will lead to collapse, so a minimum rate of '0' hits and a maximum rate of false alarms '1' are likely to be attained (p = 0 and p = 1). When both hit rates and false alarms are extreme values, the corresponding *d'* can still being calculated, however, if only one of these two is an extreme the computation is compromised. One of the most common ways to solve this problem is by applying the (1/2*N*) rule. Here extreme proportions of 0 or 1 are exchanged by the values obtained in 1/(2*N*) and 1−1(*2N*) where N is the number of similar and different trials. By dividing by 2 the total number of trials it is possible to create 'virtual halves' of a single hit rate and false alarm. However, this approach may

lead to biases on the final computations by over- as well as underestimating the population *d'*. A preferred approach is to use the so-called log-linear rule for which each cell frequency in the contingency table is increased by 0.5. More explicitly, this implies adding 0.5 to each cell in the 2x2 table where the proportion of hit rates and false alarms are calculated and by correcting the values in the formulae to obtain d' (for full details, see Hautus, 1995). This latter approach is implemented several times across the following behavioural experiments.

Participants' reaction time. In analogy to the use of *d',* the way in which different manipulations and corresponding factors influence reaction time (RT) can be used to investigate those processes generating and modulating RTs. In the current chapter, *experiment 2* and *3* include recordings of participants' verbal responses (i.e., '*yes / no'* answers to whether or no the test and memory array were similar).

The pre-processing of RTs was made before the subsequent analyses. First, error trials were discarded: since the correctness of the response is concurrent to the observation, it is assumed that RTs in error trials reflect an "atypical" train of processes. Given the uncertainty of what process is measured in error trials of standard RT paradigms, experimenters normally analyse only right trials; the same principle is assumed in EEG studies. Secondly, the data were cleaned via removal of outlying data: very short RTs (<100ms) were probably initiated before the actual onset of the test array; that is, they were anticipatory. Similarly, most simple tasks take between 700 and 1000ms to be accomplished; long RTs (>2000ms) in the current experiment would probably reflect attentional shifts or sampling error. In *Exp 2* and *3* trials containing RTs below 100ms or beyond 2000ms were removed from further analyses.

Lastly, it is important to highlight that distribution of RTs in paradigms comprising very simple tasks are fairly symmetrical whereas distributions from tasks combining memory and perceptual decisions are usually skewed (i.e., bounded on the left side but not to

the right). When skewed distributions are analysed, the median is preferred over the mean because the median and the sample medians around the true value are less sensitive to extreme values. However, under conditions of small samples and unequal sample sizes, using the median may well bias the results, and subsequently, upcoming conclusions about participants' performance (Miller, 1988). Similar to other WM experiments examining processing of body-related information (see for instance Vicary et al., 2014; Ding et al., 2015) and given that each memory load provides different number of right trials (decreasing right trials with higher memory load) analyses of RTs were based on mean average.

5.2.2.3. Results and discussion Exp.1

5.2.2.3.1. Indexes of sensitivity and bias

All data from the congruent trials (i.e., encoding right hands/moving right hand and *vice versa*) were combined. Similarly, data from the incongruent trials (encoding right hands/moving left hand and *vice versa*) were also merged. Then, hit rates, false alarms, sensitivity index D-prime, and bias index *C* were calculated and subjected to analysis of repeated measures ANOVA with factors *congruency* (congruent, incongruent) and *memory load* (holding in memory 1, 2, or 3 items).

Hit rates

Contrary to our predictions, participants' proportion of hits rate was higher when moving the hand matching the laterality of those to-be-remembered (e.g., moving left and encoding left hands). The main effect of congruency reached statistical significance ($F_{(1,9)} = 7.052$, $p = 0.026$). On average, participants in the incongruent condition reached a hit rate of .77 compared to the .82 hit rate in congruent trials. Regarding memory load, results showed a main effect ($F_{(1,9)} = 18.847$, $p < 0.001$) that did not interact with congruency ($F_{(1,9)} = 1.555$, $p = 0.238$). Subsequently, independently of the

number of hands presented in the study phase (i.e., 1, 2, or 3), the effect of congruency on hit rates was equally present during this task.

False Alarms

Independently of moving left and/or right hands and encoding left and/or right hands participants' proportion of false alarms did not differ ($F_{(1,9)} = 0.416$, $p = 0.535$). As expected, the effect of load was found to be significant ($F_{(1,9)} = 42.814$, $p < 0.0001$) whereas the interaction between congruency and load factors did not reach significance ($F_{(1,9)} = 0.136$, $p = 0.874$).

Bias - C

Despite the effect of congruency approaching significance ($F_{(1,9)} = 4.048$, $p = 0.07$), the effect of load and the interaction between both factors was not significant, ($F_{(1,9)} = 0.026$, $p = 0.974$) and ($F_{(1,9)} = 0.248$, $p = 0.783$), respectively. Interestingly, the increasing cognitive demands associated with greater memory load did not modulate the drift of participants towards responding '*yes*', which in this particular case refers to participants reporting that stimuli presented in the the memory and test arrays are similar.

Sensitivity - d'

The sensitivity index Dprime in load 1 and load 2 was very similar to those observed in the previous EEG studies of this work (i.e., around 2.2 for memory load one and approximately 1 for memory load two). In load 3 the participants' capacity to retain in memory the items decreased substantially, with an average *d'* of .39 collapsed across congruent and incongruent conditions. Nevertheless, this performance deviated from zero (i.e., null capability to distinguish trials) ($t_{(9)} = 3.827$, $p = 0.004$).

Participants' discrimination between signals (stimuli) and noise (no stimuli) was similar regardless the congruency of the hands movements and the laterality conveyed in the hands to-be-remembered. While there was a predictable and strong main effect of

memory load ($F_{(1,9)} = 80.028$, $p < 0.0001$), no effect of congruency ($F_{(1,9)} = 0.639$, $p = 0.445$) or interaction between these two factors were found ($F_{(1,9)} = 0.524$, $p = 0.601$).

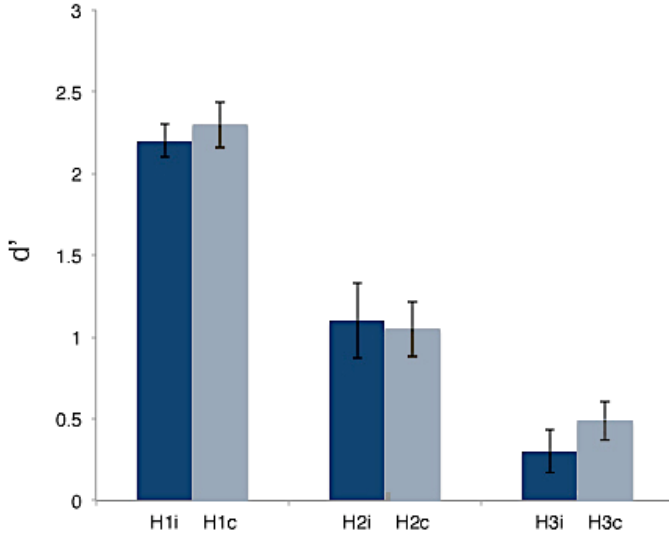


Figure 5-2. d' results in all conditions Exp1. Dark blue represents the incongruent condition, light blue represent the congruent condition. Overall performance in the hand stimulus conditions was similar and no significant differences were found between performance in memory load 1, 2, and 3 regardless congruency of the suppression; *n*=10. D-prime: sensitivity index, d' = Z (hit rate) – Z (false alarm rate); H1I and H1C (one hand to-be-remembered, incongruent and congruent condition, respectively); error bars represent within subject SEMs.

The results of *Experiment 1* are summarised in table 5-2. The results showed that participants' performance did not differ depending on whether they moved or not the same hand than those items to-be-remembered. Specifically, encoding, retaining, and retrieving left and right hand images from WM while respectively moving left and right hands did not differ from doing the same in the absence of matching between the laterality of the movement and the hand images (i.e., moving left hand-encoding left hands). These results are in line with those of Smyth and Pendleton (1989), who showed that either encoding left or right hand movements while exerting motor suppression only with the right hand yielded similar results. Overall, these results hint towards a WM system for body-related information, underpinned by sensorimotor brain

areas, that does not completely care about the processing of body-related lateralised information. However, these accounts are difficult to tease apart in the context of the present experiment because it did not include a condition absent of suppression, as well as a condition with non-body-related stimuli. The following two experiments consider these latter manipulations and add the online monitoring of the motor suppression and the additional recording of reaction times.

Table 5-2

Means and Standard Errors (SE) for Hit Rate, False Alarm Rate, sensitivity d', and bias C in all conditions of Experiment 1

Suppression	Load	Hit	FA	*d'*	*C*
Incongruent	1	.91 (.02)	.23 (.03)	2.16 (.11)	-.30 (.10)
	2	.77 (.05)	.42 (.05)	1.09 (.24)	-.33 (.13)
	3	.66 (.05)	.55 (.04)	.30 (.14)	-.29 (.11)
Congruent	1	.93 (.02)	.24 (.04)	2.31 (.15)	-.39 (.11)
	2	.80 (.04)	.46 (.06)	1.05 (.18)	-.41 (.13)
	3	.74 (.03)	.57 (.04)	.49 (.12)	-.44 (.09)

Note. Standard errors are in parentheses

5.2.3. Experiment 2

The absence of congruency effect between the laterality of perceivers' hand movement and the hands to-be-remembered in *Experiment 1* could be due to a lack of influence of the motor suppression. It is possible that just squeezing a stress ball at a constant rhythm does not exert enough interference to reveal a rather weakly specific contralateral effect. In *Experiment 2* I explored similar hypotheses that those of *Exp. 1*, namely: whether or not contralateral sensorimotor cortices play a specific and causal role in the effective encoding and maintenance of body-related information. However, three modifications were implemented: (1) the difficulty of the motor suppression was greater than that of *Exp.1*. Since previous studies have shown trade-off effects between memory performance and motor performance (see Woodin and Heil, 1996; table 5-1), in

Exp.1 participants could have interrupted or changed the rhythm of the motor suppression while encoding the stimuli. (2) In the current experiment participants were trained to keep a constant suppression with a metronome and the suppression was visually monitored with cameras during the whole experiment. (3) Contrary to *Exp.1*, the control non-body-related stimuli (polygonal shapes) were also included in the next two experiments. (4) In addition to the previous experiments, reaction times measured from the onset of the test array were measured in all conditions. By implementing these additional manipulations and control measures we expect to enhance the capacity of the experiment to assess underlying mechanisms of sensorimotor processing.

5.2.3.1. Methods

Participants

In experiment 2, thirty-two participants that did not take part in the previous experiment (18 females; mean age = 20) with normal or corrected-to-normal vision took part and gave informed consent for this experiment, approved by City, University London Psychology Department's Research Ethics Committee. From these participants a total of 8 were excluded from further analyses because due to an error in the hardware responses were not correctly recorded and/or because participants did not reach *d'* values of 1 in at least one of the conditions with memory load 1. It is important to stress that in the previous studies the values of *d'* at individual levels did not normally fall bellow 1. Therefore a total of twenty-four participants were included in further analyses.

Stimuli, experimental design, and procedure

The stimuli and procedure used in Experiment 2 were similar to those used in Experiment 1, except for 1) the very specific type of sensorimotor suppression and 2) the inclusion of shapes as control stimuli. Here participants were instructed to continuously touch one by one the tip of the thumb with each one of the remaining fingers' tips. This movement always started by connecting the thumb and the index

finger and finished by meeting the thumb and the pinky's tips. Once all fingers' tips met, the movement was restarted in the same direction and frequency (with hands in palm up position, moving more lateral to central fingers, i.e., from index to pinky) (Fig. 5-3). We expected that in comparison to the hand movement in *Exp.1*, the increasing difficulty of the present movement would exhibit stronger interfering effects.

In order to control the frequency and subsequent speed of the sensorimotor suppression, participants were instructed to produce 28 touches in each finger by minute, which are around 140 single touches per minute. This was done by training participants to carry on the WM task while listening to a digital metronome at 140BPM (beats per minute). Once the participants felt comfortable doing the dual task, the metronome was switched off and the recording of participants' responses started while the movement was maintained until the next break. Lastly, given that previous studies have shown a trade-off between accuracy of body movements and body-related memory tasks, it was important to monitor that participants maintained a constant pace in the motor suppression during the whole experiment. In order to monitor participants' hand movements, several lights and cameras were incorporated under the black opaque surface covering the hands from the participants' eyesight.

As in the previous experiments of this PhD thesis, participants were counterbalanced across stimuli conditions: half of the participants completed first all trials in the hand stimulus condition whereas the other half of participants completed first the shape stimulus condition. Experiment 2 had a total of 504 trials, this is equal to 252 trials by stimulus condition, including 84 trials in each memory load (1, 2, and 3). In random order of presentation, half of the trials comprised the task-irrelevant sensorimotor suppression in congruency with the laterality of the stimuli to-be-remembered (congruent condition), the other half of trials involved an incongruent matching between the moving hand and the hands to-be-remembered (incongruent condition).

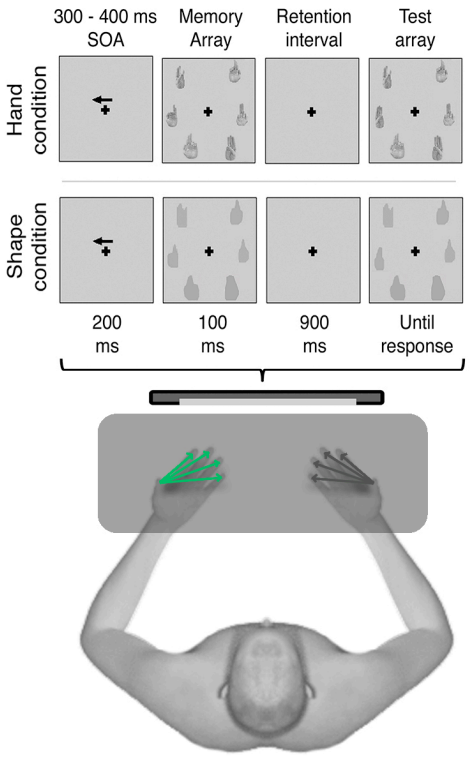


Figure 5-3. Task design and procedure Exp.2. On 50% of the trials participants encoded left hand images while moving their left hand fingers (i.e., touching one by one the thumb with the rest of the fingers' tip) and *vice versa* (congruent trials) while in the other 50% they encoded left hand images while doing the suppression with their own right hand and *vice versa* (incongruent trials). Participants were instructed to produce a single touch between the fingertips at a constant pace of 140BMP**.** The figure depicts a *'different congruent trial - load 3'* in which hands to-be-remembered are shown in the left hemifield.

5.2.3.2. Results and discussion Exp. 2

5.2.3.2.1. Indexes of sensitivity and bias

The data was pre-processed and analysed as in *Experiment 1*. Repeated measures ANOVA with factors *congruency* and *memory load* was performed for hit rates, false alarms, *C,* and *d'*. In addition, *Experiment 2* also included factor *stimulus* (hand images and geometrical shapes). The subsequent ANOVA resulted on a 2 (congruent / incongruent) x 2 (hand / shape images) x 3 (load 1/ 2/ 3). Summary of all data is presented in table 5-4.

Hit rates

In comparison to *experiment 1* the overall proportion of hit rates was slightly smaller, especially in load 1 and load 2. Conversely, when encoding three stimuli the proportion of hit rates in both experiments was very similar (approximately 0.75 regardless stimuli and condition).

Beyond the already expected main effect of load ($F_{(2,46)} = 28.555$, $p < 0.0001$), no other main effects or interactions were found, namely, nor stimuli ($F_{(1,23)} = 0.772$, $p = 0.389$) or congruency exhibited significant effects ($F_{(1,23)} = 0.141$, $p = 0.710$), as well as the double interactions between factors stimulus type and congruency ($F_{(1,23)} = 0.348$, $p = 0.561$), stimulus and load ($F_{(1,23)} = 0.189$, $p = 0.828$), and congruency by load ($F_{(1,23)} = 0.375$, $p = 0.689$) did not reach significance. Similarly, the triple interaction between all factors did not show differences modulated by the corresponding factors ($F_{(2,46)} = 1.876$, $p = 0.165$).

False Alarms

Inspection of the previous and current experiment indicates that overall participants made similar proportions of false alarms in all memory loads (steadily increasing across loads from 0.23 to 0.56). The subsequent analyses revealed a near significant main effect of stimulus type ($F_{(1,23)} = 3.456$, $p = 0.075$), a significant main effect of load ($F_{(1,23)} = 133.838$, $p < 0.0001$), and a double significant interaction between these two latter factors: stimulus by load ($F_{(2,46)} = 7.828$, $p = 0.001$). Follow-up t-test revealed that such interaction was driven by a significant difference with higher number of false alarms in the hand condition *vs.* shape stimulus condition ($t_{(23)} = 3.023$, $p = 0.006$). No other main effects or interactions were found (*all ps* > 0.493).

Bias - C

Overall it was found a *C* value between -0.28 and -0.4 that was present in all conditions regardless the remaining factors congruency, load, and stimulus. The general tendency of participants to respond 'yes' (i.e., stating similarity between memory and test arrays)

was equal to that in experiment 1. Despite the results of experiment 1 showing a close to significant effect of congruency between participants' hand movement and stimuli to-be-remembered, here the effect of congruency on ones' bias was far from significant ($F_{(1,23)} = 0.435$, $p = 0.516$). Interestingly, while in the earlier experiment memory load did not influence participants' bias, in the current experiment a significant main effect of memory load was a found ($F_{(2,46)} = 9.720$, $p < 0.001$). No other main significant effects or interactions were found (all *ps* > 0.129).

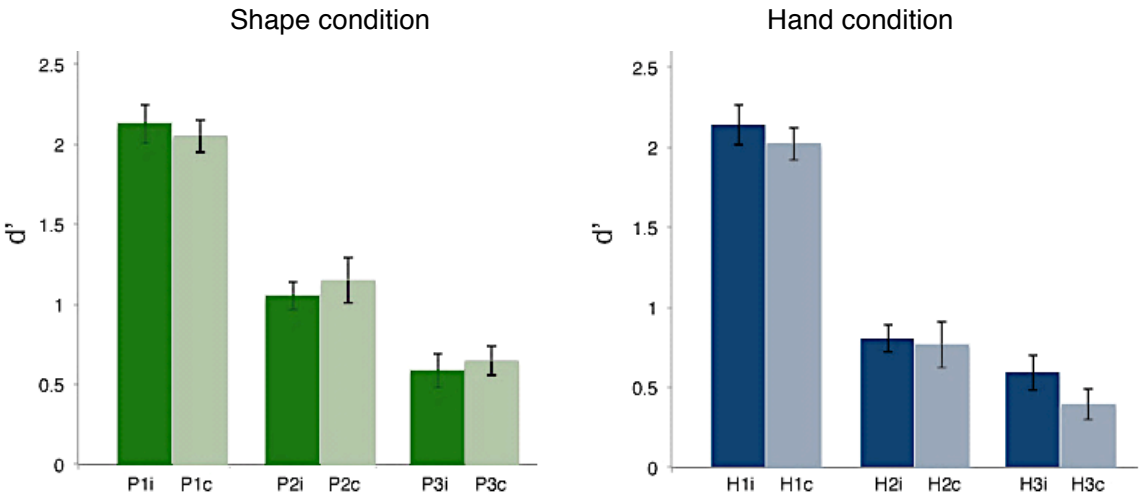


Figure 5-4. d' results in all conditions. Dark colours represent the incongruent condition, light colours represent the congruent condition. Overall performance in the hand and shape stimuli conditions was dissimilar ($p < 0.05$). However, the effect was found regardless the memory load and suppression conditions. *n*=24; D-prime: sensitivity index, d' = Z (hit rate) – Z (false alarm rate); P1I and P1C (one shape to-be-remembered, incongruent and congruent condition, respectively); error bars represent within subject SEMs.

Sensitivity - d'

Extreme values of hit rates and false alarms were corrected by the log-linear rule (Hautus, 1995) (*see Methods Exp.1)*. Participants' sensitivity to distinguish the presence of signal and noise (i.e., old/new, similar/different stimuli) in load 2 and 3 was slightly smaller than that found in experiment 1. This was more evident in the hand stimulus conditions: regardless of the congruency between the participants' movement and

laterality of the hands to-be-remembered, *d'* values were constantly below 1. This is reflected in the near significant double interaction between stimulus type and memory load ($F_{(1,23)} = 2.974$, $p = 0.061$) and the significant main effect of stimulus condition ($F_{(1,23)} = 6.931$, $p = 0.015$). The remaining effects and interactions did not approach significance (all *ps* > 0.307) (Fig. 5-4).

5.2.3.2.2. Reaction times

After pre-processing of RTs (see methods in *Experiment 1* for full explanation) the mean of all participants' verbal responses were found between 850 and 1000ms after onset of the test array. Here only a significant main effect of memory load was found ($F_{(2,46)} = 58.868$, $p < 0.0001$). This effect exhibited a steady increasing in reaction time with greater memory loads. The remaining factors i.e., stimulus ($F_{(1,23)} = 0.781$, $p = 0.386$), congruency ($F_{(1,23)} = 0.001$, $p = 0.981$), and all possible interactions between factors did not reach significance (all *ps* > 0.392). Overall the analyses of RTs indicate that hand movements performed with either the left or right hand do not modulate the concurrent encoding of hand images that match the laterality of such hand movements nor the encoding of non-body-related shape images (Fig. 5-5) (which do not convey such lateralized representations).

The overall results of *Experiment 2* are summarised in table 5-3. After increasing the sample size, enhancing the motor suppression, measuring RT, and including the control shaped stimuli, the results showed that similar to *Experiment 1,* participants' performance did not differ whether their lateralized movement matched or not the laterality of the left or right hands to-be-remembered. The absence of motor suppression was also observed in the shapes stimuli condition.

Furthermore, the RT in both stimuli conditions did not reveal any interaction with memory load (Fig. 5-3). The only relevant significant difference was found as a main effect of stimulus condition in the participants' sensitivity *d'.* Regardless of memory load

and congruency, the overall *d'* was lower in the hand stimulus conditions (*M* = 1.12*, SD = .33)* than in the shape stimulus condition (*M* = 1.27*, SD* = .29). The main effect of stimulus condition, the ubiquitous effect of memory load, and the lack of interaction between these factors and the congruency of the motor suppression suggest that such suppression is equally present or equally absent. Since the past two experiments did not include a no-movement condition such possibility is difficult to tease apart. Therefore, *Experiment 3* includes a movement factor with two levels: movement and no-movement.

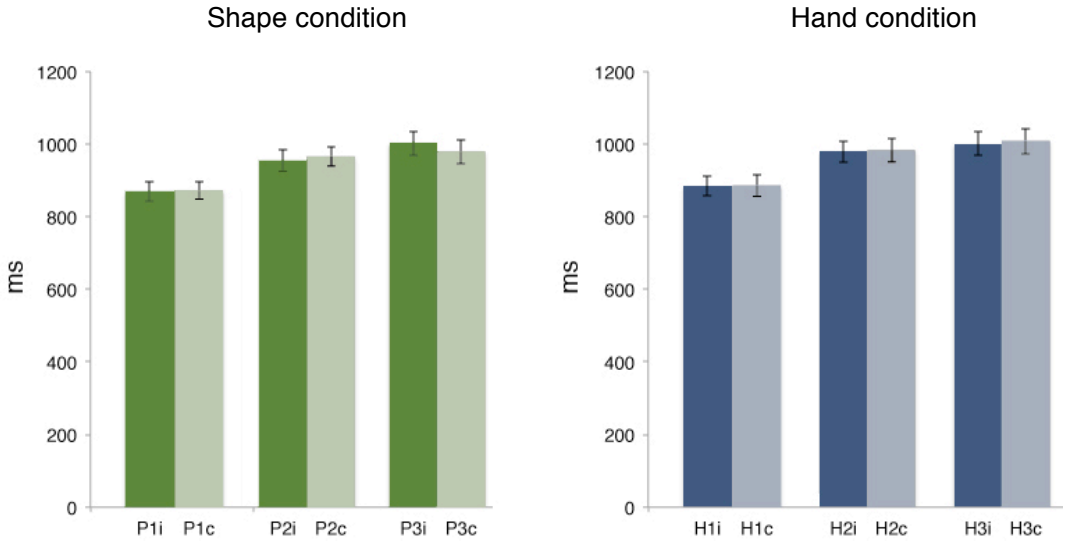


Figure 5-5. Reactions times in all conditions Exp.2. Dark colours represent the incongruent condition, light colours represent congruent condition. Overall performance in the hand and shape stimuli conditions was similar and no significant differences were found between memory loads 1, 2, and 3 regardless the congruency of the suppression. *n*=24; P1I and P1C (one shape to-be-remembered, incongruent and congruent condition, respectively); ms: milliseconds; error bars represent within subject SEMs.

Table 5-3

Means and Standard Errors (SE) *for Hit Rate, False Alarm Rate, sensitivity d', bias C, and reaction times in all conditions of Experiment 2*

		Shape condition					Hand condition				
Sup	Lo	Hit	FA	*d'*	*C*	*RT*	Hit	FA	*d'*	*C*	*RT*
Inc	1	.88 (.01)	.23 (.03)	2.13 (.12)	-.22 (.08)	869 (27)	.86 (.02)	.19 (.02)	2.14 (.12)	-.14 (.06)	885 (28)
	2	.77 (.02)	.40 (.02)	1.05 (.09)	-.25 (.05)	956 (30)	.73 (.03)	.45 (.03)	.81 (.10)	-.28 (.06)	979 (29)
	3	.73 (.03)	.55 (.03)	.58 (.11)	-.43 (.08)	1000 (33)	.77 (.03)	.59 (.03)	.59 (.13)	-.53 (.07)	1001 (32)
Con	1	.88 (.02)	.25 (.02)	2.05 (.10)	-.30 (.07)	872 (23)	.87 (.01)	.22 (.02)	2.02 (.11)	-.20 (.05)	885 (29)
	2	.75 (.03)	.37 (.03)	1.15 (.14)	-.22 (.07)	966 (26)	.75 (.03)	.48 (.03)	.077 (.09)	-.34 (.07)	984 (32)
	3	.76 (.03)	.55 (.03)	.65 (.09)	-.47 (.08)	979 (34)	.72 (.03)	.58 (.03)	.39 (.10)	-.43 (.08)	1008 (35)

Note. Standard errors are in parentheses; Sup: suppression; Lo: memory load; Inc: incongruent, Con: congruent; RT in milliseconds.

5.2.4. Experiment 3

Experiment 2 suggests that congruency effects between the laterality of the perceivers' hand movement and the laterality of hands to-be-remembered do not exert a strong influence in the participants' ability to remember body and control non-body-related information. The *d'* values of *Experiment 2* seem to indicate a main effect of stimulus type, where the overall sensitivity towards hand stimuli was lower than that for shapes stimuli. There is a lack of interaction between the congruency of such suppression, the type of encoded stimuli, and the memory load. Smyth and Pendleton (1989) showed that performing a motor suppression with either the left or right hand decreased memory span for hand postures of right hands (table 5-1). Conversely, a spatial suppression also performed with the left or right hand did not decrease such memory span. Therefore, it is possible that the motor suppression in Exp.2 was exerting a general interference, which is independent of the hand generating the hand movement/suppression. However, this hypothesis is difficult to tease apart because Exp.2 did include a non-suppression condition.

In *Experiment 3* I asked whether or not sensorimotor cortices play a more general and causal effect in the effective encoding and maintenance of body-related information. To

this aim, the unimanual motor suppression of the previous experiment was performed simultaneously with both hands. Therefore, the key factor here is the presence or absence of motor suppression. By implementing this manipulation we expect to exhibit a more general involvement of the sensorimotor system (i.e., somewhat independent of the laterality and effector) on specifically holding in WM images of body but not body-related stimuli.

5.2.4.1. Methods

Participants

In experiment 3, fourteen new participants (9 females; mean age = 21) with normal or corrected-to-normal vision took part and gave informed consent for this experiment, approved by City, University London Psychology Department's Research Ethics Committee. Three participants were excluded due to low performance in memory load 1 ($d' < 1$). Neither in the very first pilot nor in the later EEG studies did the participants' sensitivity usually all below 1.

Stimuli, experimental design, and procedure

The stimuli and procedure used in Experiment 3 were similar to those used in Experiment 1 and 2, except for the specific movement conditions. In Experiment 3 participants were instructed to perform the same sensorimotor suppression as in Experiment 2, but simultaneously with both hands and in only half of the trials. These conditions were implemented in counterbalanced blocks.

Experiment 3 included a total of 504 trials, this is equal to 252 trials by stimulus condition, including 84 trials in each memory load (1, 2, and 3), half comprising the task-irrelevant sensorimotor (*movement* condition) and half without it (*no-movement* condition). As the previous experiments of this thesis, participants were counterbalanced between stimulus conditions. Moreover, blocks containing the motor interference (movement condition) were also counterbalanced across the experiment.

The number of hand or shape images to-be-remembered was randomly selected across trials.

5.2.4.2. Results and discussion Exp. 3

5.2.4.2.1. Indexes of sensitivity and bias

The data was pre-processed and analysed as in *Experiment 1* and *2*. Repeated measures ANOVA with factors *stimuli* and *memory load* was computed for hit rates, false alarms, sensitivity index *d'*, and bias index *C.* However, in the current experiment there was no congruency factor, instead the presence of *movement* (i.e., moving or not both hands while encoding stimuli) was the third factor. The corresponding ANOVA followed a 2 (movement / no-movement) x 2 (hand / shape images) x 3 (load 1/ 2/ 3) design.

Hit rate

The overall proportion of hit rates was higher in the no-movement condition than in the movement condition: results showed a significant main effect of the factor movement ($F_{(1,10)} = 28.555$, $p = 0.021$). Nevertheless, participants' movement did not interact with any other factors, namely: movement x stimulus ($F_{(1,10)} = 1.777$, $p = 0.212$), movement x load ($F_{(2,20)} = 0.678$, $p = 0.519$), stimulus x movement x load ($F_{(2,20)} = 0.812$, $p = 0.458$). The only main effect reaching significance was load ($F_{(2,20)} = 17.493$, $p < 0.0001$) which showed a decreasing proportion of hit rates with increasing number of stimuli to-be-remembered.

False Alarms

Overall false alarms in the present experiment was slightly higher than the previous two experiments. Here the false alarms ranged from 0.24 to 0.61 (compared to the 0.23 to 0.56 of the previous experiments). Moreover, the descriptive statistics exhibit a general difference between the proportions of false alarms in the hand stimulus conditions compared to the shape stimulus condition. However, further inspection of such

difference indicates no differences between encoding of hands and shapes in WM ($F_{(1,10)} = 3.424$, $p = 0.094$). Then, besides the predictable load effect ($F_{(2,20)} = 80.777$, $p < 0.0001$), only an interaction between movement and load (regardless of stimuli types) approached significance ($F_{(2,20)} = 3.107$, $p = 0.067$). All the remaining effects and interactions were not significant (i.e., greater than 0.130).

Bias - C

The *C* values in experiment 3 ranged from -0.30 to -0.53 (compared to the -0.28 to -0.4 found in the previous experiments). Once again it was found that participants tend to respond 'yes' (i.e., reporting that both memory and test arrays were similar). Despite the previous experiments finding some differences, here no main effects or interactions yielded significant differences (*all ps* > 0.090). Only two 'occurrences' seemed to slightly modulate participants' bias: the increasing memory load and its further modulation with ones' hand movement, however, these factors did not reach significance ($F_{(2,10)} = 2.734$, $p = 0.089$ and $F_{(2,10)} = 3.128$, $p = 0.094$, respectively)

Sensitivity - d'

Participants' sensitivity to discriminate the stimuli between the memory and test arrays was examined. The means across all conditions showed that in general the movement of both hands impaired participants' performance (Fig. 5-6). The factor movement was found to be significant ($F_{(1,10)} = 7.004$, $p = 0.024$). In other words, the conjunction of hit rates and false alarms that is considered in *d'* was modulated by the motor suppression in the form of a bimanual hands movement. Next, results showed a significant main effect of memory load ($F_{(2,20)} = 80.777$, $p < 0.0001$), which exhibited decreasing *d'* with increasing memory load regardless of the presence of hands movement during encoding of both hand and shape stimuli. Lastly, the results from the triple interaction between stimulus, load, and movement did not reach significance ($F_{(2,10)} = 2.454$, $p = 0.111$). In similar a vein, all other factors and interactions did not reach significance:

stimulus ($F_{(1,10)} = 1.727$, $p = 0.218$), stimulus X movement ($F_{(1,10)} = 1.455$, $p = 0.256$), stimulus X load ($F_{(2,20)} = 1.504$, $p = 0.246$), and movement X load ($F_{(2,20)} = 1.015$, $p = 0.380$).

Table 5-4

Means and Standard Errors (SE) *for Hit Rate, False Alarm Rate, sensitivity d', bias C, and reaction times in all conditions of Experiment 3*

		Shape condition					Hand condition				
Sup	Lo	Hit	FA	*d'*	*C*	*RT*	Hit	FA	*d'*	*C*	*RT*
NoM	1	.95 (.02)	.25 (.03)	2.24 (.16)	-.39 (.09)	786 (38)	.85 (.05)	.23 (.03)	2.03 (.25)	-.20 (.09)	785 (.35)
	2	.81 (.03)	.47 (.04)	1.06 (.16)	-.44 (.09)	855 (39)	.79 (.05)	.52 (.04)	.85 (.18)	-.49 (.12)	832 (25)
	3	.82 (.03)	.53 (.03)	.92 (.14)	-.53 (.08)	893 (43)	.76 (.03)	.62 (.05)	.40 (.19)	-.53 (.07)	854 (28)
Mov	1	.83 (.03)	.31 (.05)	1.59 (.15)	-.25 (.12)	872 (41)	.84 (.02)	.31 (.05)	1.71 (.19)	-.29 (.15)	828 (34)
	2	.77 (.03)	.42 (.04)	1.01 (.18)	-.30 (.09)	913 (46)	.72 (.04)	.52 (.06)	.57 (.19)	-.34 (.10)	931 (33)
	3	.69 (.04)	.54 (.04)	.43 (.14)	-.31 (.08)	954 (44)	.70 (.03)	.56 (.03)	.46 (.13)	-.39 (.12)	958 (40)

Note. Standard errors are in parentheses; Sup: suppression; Lo: memory load; Mov: movement condition; NoM: no movement condition; RT in milliseconds.

5.2.4.2.2. Reaction time

RTs data was pre-processed as in *Experiment 2.* Then, mean reaction times of all participants' verbal responses were found to be between 780 and 960ms after onset of the test array (approximately 60ms faster than in experiment 2). Similar to the majority of parameters computed in the current behavioural experiments, the results of the ANOVA showed a main effect of memory load ($F_{(2,20)} = 27.377$, $p < 0.0001$). However, while in *experiment 2* only load seemed to modulate the time needed for the participants to respond, here the presence of hands movement while encoding and maintaining the stimuli to-be-remembered also modulated participants' performance ($F_{(1,10)} = 14.285$, $p < 0.004$).

Interestingly, a triple interaction between stimulus x movement x load was also found ($F_{(2,20)} = 4.180$, $p = 0.030$). The follow-up of this interaction by stimuli types showed significant main effects in the hand stimulus condition for both movement and load

factors ($F_{(1,10)} = 11.973$, $p = 0.006$; $F_{(2,20)} = 21.107$, $p < 0.001$, respectively), as well as a significant interaction between these two factors ($F_{(2,20)} = 3.925$, $p = 0.036$). Follow-up t-tests showed significant differences in load 2 and load 3, but not in load 1 when moving both hands (Fig. 5-7). Specifically, holding in memory 2 and 3 hand images while performing the motor suppression led to slower RTs than carrying the memory task alone ($t_{(10)} = 3.212$, $p = 0.009$, $t_{(10)} = 4.100$, $p = 0.002$, respectively). In the shape condition, the results also showed a main effect of movement ($F_{(1,10)} = 12.177$, $p = 0.006$) and memory load ($F_{(2,10)} = 18.387$, $p < 0.0001$), but no interaction between them was found ($F_{(2,20)} = 0.908$, $p = 0.419$).

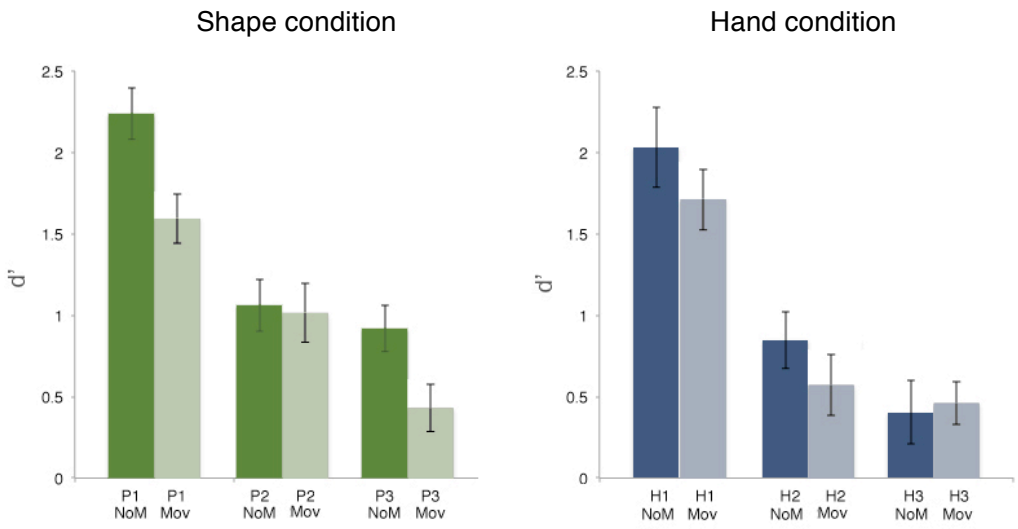


Figure 5-6. d' results in all conditions. Dark colours represent the no-movement condition, light colours the movement condition. Overall performance in the hand and shape stimuli conditions was similar. No interactions between stimuli conditions, load, and movement were found. *n*=11; D-prime: sensitivity index, d' = Z (hit rate) – Z (false alarm rate); P1NoM and P1MoV (one shape to-be-remembered, no movement and movement condition, respectively); error bars represent within subject SEMs.

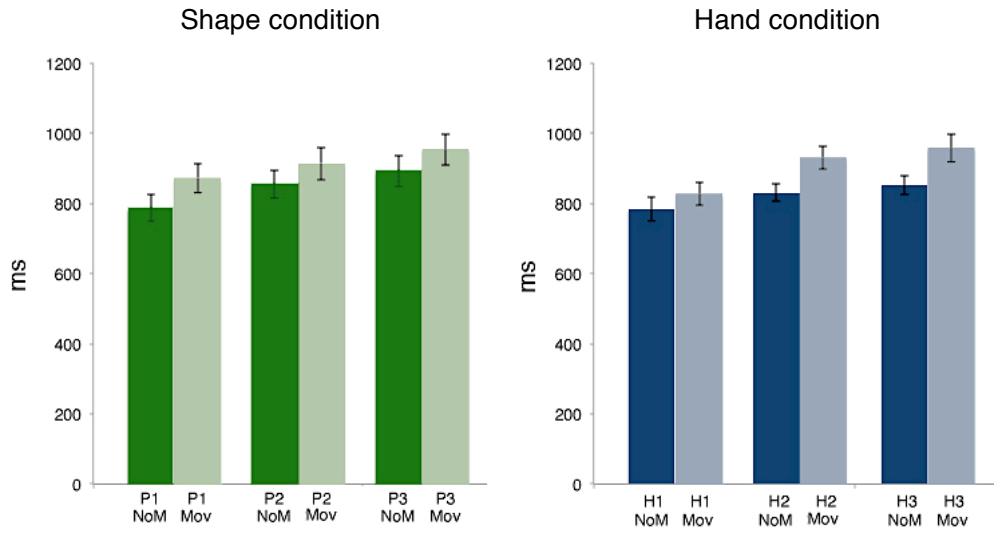


Figure 5-7. Reactions times in all conditions. Dark colours represent the no-movement condition, light colours represent movement condition. Responses in the hand stimulus condition were slowed down as memory load increased (i.e., stimulus condition X memory load X movement presence, followed by memory load X movement in the hand stimulus condition only). *n*=11; ms: milliseconds; P1NoM and P1MoV (one shape to-be-remembered, no-movement and movement condition, respectively); error bars represent within subject SEMs.

The analyses of memory performance in *Experiment 3* did not yield significant results. Beyond the expected main effect of load, values of *d'*, including its corresponding components, did not show main effects neither interactions. Further, it was found a reduction of participants' sensitivity to discriminate the stimuli regardless the stimulus type condition. A significant main effect of movement was found without any further interactions. Nevertheless, the analyses of RTs revealed a significant triple interaction (i.e., stimulus type X memory load X movement) where only the hand stimuli elicited slower responses across memory loads that were concomitant to the movement of the motor suppression. These latter results highlight the possible presence of a trade-off effect in participants' performance; an effect already observed in Smyth and Pendleton (1989) and Woodin and Heil (1996).

5.3. General discussion

In the present study we sought to interfere with the on-going sensorimotor processing during a WM task for body and non-body-related images, exploiting the contralateral disposition of the sensorimotor cortex by using manual and bimanual motor suppression. We tailored the EEG experiments (*Chaper 3* and *4)* to three different behavioural experiments, 'inducing impairment' of sensorimotor processing by means of a sensorimotor suppression: i) in *Experiment 1* participants' held in memory left or right hand images while moving the hand matching or not the laterality conveyed in the visual display (i.e., unimanual congruent/incongruent motor suppression). ii) *Experiment 2* was similar to the first but included the control shape stimulus condition, enhanced and monitored suppression, and measures of RTs. iii) *Experiment 3* was similar to *Exp. 1* and *2* but motor suppression was present in form of a bimanual task, but only in 50% of the trials.

The results revealed an expected effect of memory load, which was present across the three experiments, mainly in the proportion of hit rates and *d'. Exp.1* exposed a lack of main effects and interactions; contrary to our initial hypothesis, the congruency of the movement matching the hands to-be-remembered did not modulate participants' performance. In *Experiment 2* the results showed a main effect of stimulus condition. The overall sensitivity to distinguish old and new stimuli between the memory and test arrays was somewhat lower in the hand stimulus condition compared to the shape condition. Interestingly, the main difference between *Exp.1* and *2* was the increasing difficulty of motor suppression. The motor suppression in the second experiment required, in principle, higher motor control and tactile processing. The lower performance in the hand stimulus condition could be due to an overall effect of the suppression, priming the underlying mechanisms of the single task too. The results of these experiments show that the effect of the

suppression seemed general and irrespective of the matching laterality between the stimuli and the perceivers' actual movement.

In *Experiment 3* we tested participants without the motor suppression, which showed that performance dropped in the dual task compared to the single task condition in both stimuli conditions. Despite no other effects or interactions being found in the proportion of hit rates, false alarms, *d',* and *C*, analyses of the reaction times revealed slower responses with increasing memory load and motor suppression (i.e., stimuli X memory load X task movement interaction). The follow-up analyses exhibited that RTs of verbal responses, indicating similarities/differences between arrays, increased with memory load in the hand stimulus condition (i.e., in memory load 2 and 3, but not 1).

Our results are consistent with Smyth and Pendleton (1989), who found a double dissociation between the type of suppression task and memory performance. One of the suppression conditions included participants squeezing a tube. The second suppression task involved a spatial tapping task. Squeezing a tube with either the left or right hand, varying the position of the hand, decreased memory span for hand movements presented with either the left or right hand. Conversely, performing a spatial tapping task with either the left or right hand interfered with the memory span for spatial locations but did not affect memory span for movement patterns. Therefore, suppression was task/stimuli-driven but irrespective of the effector. Moreover, Smyth and Pendleton (1989) also showed that execution of suppression tasks is slower when paired with the matching memory tasks (spatial suppression – spatial memory task). In *Experiment 3,* RTs in the hand stimulus condition increased with memory load during the motor suppression. This interaction could reflect trade-off effects in which decelerating responses allow better sensitivity (i.e., *d'* values).

Such trade-off could explain the lack of differences in performance between stimuli conditions in *Experiment 3*.

5.3.1. Absence of contralateral effects in processing WM for sensorimotor information?

The present experiments barely suggest that motor suppression may affect WM for visually perceived body-related information. Interestingly, the mechanisms for such processes do not seem that well contralateralised. Performance in trials where participants encoded right hand images while moving the right hand was similar to those trials where they encoded also right hands but moved the left hand and *vice versa.*

Considering the absence of contralateral effects in the current experiments, how is it possible that some studies (including our previous EEG studies) found contralateral processing of body-related information? The degree of contralateralisation seems to vary from moving/sensing one's body to the perception and memory representation of others' bodies. First, sensorimotor cortex is well contralateralised depending on the body part; the sense of feeling/moving one's right hand is mostly underpinned by the left somatosensory and motor cortex (i.e., upper limbs are well lateralised). Nevertheless, there are strong interhemispheric interactions linking somatosensory processing across the cortices of both hemispheres (Tame and Longo, 2015; Azañón et al., 2016)

Secondly, while it is widely recognised that particular brain regions underpin both action execution and action observation, seeing others bodies and actions does not elicit the same degree of contralateral activity that would be recorded when executing the real action. Many studies have reported lateralised activity when perceiving others bodies and actions, but this does not always imply that brain structures and ensuing activity are contralateral. For instance, studies have indicated overall and

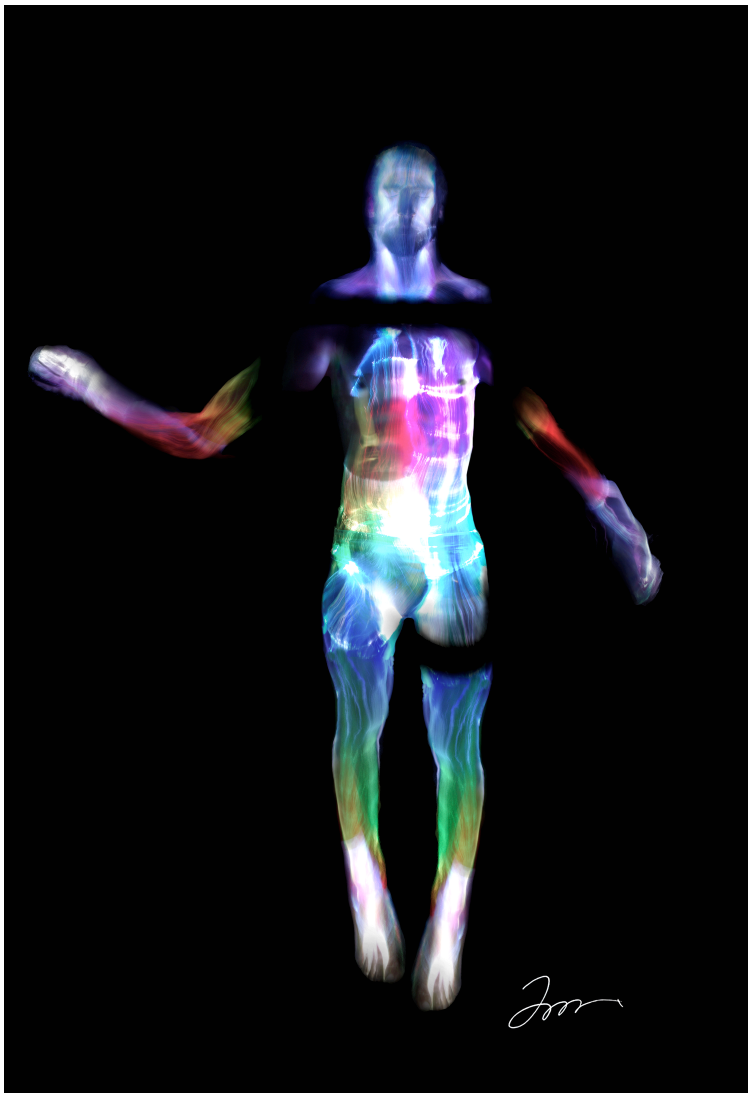
greater activity in the left sensorimotor areas regardless of the types of observed actions (Kalénine et al., 2010; Ortigue et al., 2010). On the other hand, other studies have found evidence for a more specific contralateral processing (see for instance Borghi and Cimatti, 2010). As noted in *Chapter 2*, the degree of embodiment elicited through different manipulations could explain how the brain engages in a more or less contralateralised manner. Overall, the 'gap' between what is observed (or encoded to be memorised) and the perceivers' sensorimotor state (e.g., experience, posture, task) may define a point in the continuum of contralateralised activity that is observed. Reductions of such gap, when percept and perceivers are more alike, may lead to contralateral involvement of the brain regions that are necessary to carry on the action itself. Conversely, if such distance is augmented, for instance when a naïve participant observes a skilled hand movement, brain activity might be less contralateralised (but remain lateralised). This is different from the changes in BOLD signal described by (Cross et al., 2012) who described how perceiving novel body movements can lead to increasing involvement of brain areas contributing to the perception of bodies.

5.3.2. Conclusions

The current study suggests that holding in WM information about lateralised body parts (i.e., left and right hand images) is underpinned by the sensorimotor system in a general manner rather than in a laterality-matching manner. Contrary to our hypothesis, participants' performance was similar whether they encoded left/right hands while suppressing left/right hands or right/left hands, respectively. These results are discussed in the context of the preceding EEG studies in the PhD summary of *Chapter 6*. Then, a modulation by memory load was only found in the hand stimulus condition when the motor suppression was applied to both hands. This suggests the presence of a system dealing with different features of visually

perceived body information that cannot deal with both tasks simultaneously. It could be suggested that both hands cannot be controlled independently and that the motor suppression elicits an overall interference. Thus, sensorimotor cortices may play a role in certain aspects along the encoding and maintenance of visually perceived bodily information in WM.

5.3 Artistic Impressions V



Bodily Realm – Body deconstruction or tortillas de patatas (2015) Photography on board (45 x 30cm) / AGP

If part of the memories that we create about others' bodies is mapped over the representation of our body in the brain, do we represent such bodies in a somatotopic manner? (e.g., matching the observed body as a template in our own cortical body?).

6. Chapter 6: General discussion

6.1. Introduction

In the current chapter I review the work presented in this PhD thesis. I start by summarising the overall goals of my work, as well as the specific aims of each chapter and study. Then, I recapitulate the main results of each study and, based on others' research and my own work, I reflect on the interpretation of these results. Next, I conclude this thesis by revising overall limitations, discussing some of the open questions that need to be further explored (i.e., open questions and research proposals), and by encapsulating the main findings and interpretations in a brief conclusion

6.2. Summary of background and aims

Observing, recognising, understanding, learning, and imitating others' bodily actions are fundamental processes in human interaction. To implement any of those cognitive processes, one perceives another person's action and transforms such percept into a representation that can be later updated, retained, and accessed. The transformation of body-related information into an associative form that can be later recalled in favour of prospective behaviour requires memory mechanisms.

Most of the studies in the memory domain have used arbitrary stimuli such as sequences of numbers or letters, coloured squares, lines, and shapes, allowing us to identify non-overlapping memory systems to store semantic and visuo-spatial information in WM (Baddeley and Hitch, 1974). A memory system to hold more socially meaningful stimuli such as bodies and actions was later proposed by Smyth and colleagues, who provided behavioural evidence of a system to encode, recall, and maintain others' actions in one's memory (Smyth et al., 1988,1989). Importantly, these and other studies suggested that this memory system for body-related information (e.g., visually perceived actions and body

postures) is underpinned by that neural circuitry that allow us to move and feel our own body, that is, our own body representation in the brain. Investigating these brain regions during encoding of visually perceived body stimuli is the main aim of the present thesis.

With the advent of neuroimaging and novel electrophysiological techniques, two important discoveries in the fields of perception of actions and WM have guided my PhD work. Briefly, different studies in perception of actions and bodies showed that (1) a number of brain regions are active during action observation and action execution (di Pellegrino et al., 1992; Gallese et al., 1996). Therefore, part of the cortical areas that represent our own body and actions in the brain, allowing us to move and feel our body, play a key role in perception of others' actions and bodies. Secondly, in the WM field, several studies showed that (2) brain regions contribute to perceiving and maintaining stimuli to-be-remembered in WM. Accordingly, the brain regions contributing to perception also underpin the maintenance of the percept in memory (Fuster and Alexander, 1971; Harris et al., 2002; Vogel and Machizawa, 2004; Serences et al., 2009). Those two findings suggest that brain regions with a role in perception may contribute to storing percepts beyond the perceptual stage. In the case of perceiving bodies and actions, somatosensory and motor cortices may underpin encoding and maintenance of bodily percepts beyond online perception. The examination of these brain regions during encoding of visual body-related stimuli is one of the main purposes of this thesis. In the next sections I revisit in more detail the aims and background information of the different chapters.

Background and aims of Chapter 2: Revealing hidden representations of the body in the brain. Overall, there is a good understanding on how to design experiments examining WM for arbitrary stimuli and on the perception of bodies through neuroimaging techniques. However, there is no clear approach to develop EEG studies on WM for visually perceived body stimuli.

The aim of Chapter 2 was to develop a combination of method and guideline to study perception and memory encoding of body-related images. This method is based on the ERP-EEG technique. Importantly, there are two constrains that need to be considered when applying such technique: i) ERP-EEG possesses magnificent temporal resolution but low spatial resolution. ii) Encoding body images elicits a visual response that spreads from posterior/visual to more anterior and body-related cortices (i.e., the neural candidates to process bodies in memory). This visual-evoked potential (VEP) masks brain responses that are also responsible for the processing of body-related information. Therefore, encoding and other processes linked to the transformation of bodily information onto our own cortical body representation (i.e., sensorimotor and somatosensory cortices) are difficult to dissociate from the VEPs generated at the sight of body stimuli. To solve this issue, we proposed the elicitation of a time-locked neural response in somatosensory cortex during encoding of visual information. This can be accomplished by delivering task-irrelevant tactile taps to the participants' index fingers while they encode and hold in memory different numbers of body images. The tactile tap elicits a somatosensory-evoked potential (SEP) that allows measurement of somatosensory processing, which is modulated by the type of visual information 'delivered' by the VEP. Then, by means of the subtractive method detailed in *Chapter 2* and *3*, it is possible to dissociate SEPs from concurrent VEPS. Hence, it is possible to explore the involvement of body-related cortices when seeing and encoding bodily-related information with high temporal resolution.

Background and aims of Chapter 3: Neural dissociation for visual and sensorimotor WM - somatosensory brain areas. Sustained activity has been associated with maintaining task-relevant information in WM. This sustained activity seems to arise from those perceptual brain areas that participate in processing the percept in the absence of WM demands. Moreover, this form of activity increases with the number of stimuli to-be-remembered (i.e., memory load). For instance, Vogel et al. (2004, 2005) found an enhancement of EEG

waveforms arising from posterior/visual cortex that was concomitant to the number of visually depicted shapes to-be-remembered in a delayed match-to-sample task. Harris et al. (2002) and Katus and colleagues (2014, 2015) found that memorising a greater number of tactile taps encompasses increasing brain activity over somatosensory cortex. Despite the results of those studies showing enhancement of modality-specific cortices, it is unclear if sustained activity is defined by the sensory input modality or by the perceptual encoding properties of the information to-be-remembered.

Since perception of body stimuli (e.g., hand images, but not shapes) involves brain areas beyond visual cortices (i.e., parietal/somatosensory cortices; SCx), modulation of sustained activity by memory load could be found over SCx as result of visually driven processing of hand images in WM. To explore this hypothesis, in *Chapter 3* we recorded different levels of sensory response during encoding of visual stimuli depicting hand images and shapes. Specifically, we elicited and later dissociated visual-evoked potentials and somatosensory-evoked potentials (VEPs, SEPs) by using the method detailed in *Chapter 2.* Then we examined whether or not the number of hand images to-be-remembered modulates visual cortex, as well as somatosensory regions beyond visual carry-over effects that are generated at the sight of body stimuli.

Background and aims of Chapter 4: Sensorimotor recruitment during WM for body and non-body-related images. Current models portray WM as a reestablishment of perceptual experience. Interestingly, we know from studies on action observation that body-related stimuli elicit perceptual activity beyond sensory-input streams. However, whether or not such brain regions (somatosensory and motor cortices) are also recruited during WM is still unclear.

In the previous chapter we applied a novel EEG method and developed a WM paradigm that allowed us to inspect one the neural candidates to support memory processing of

visual body images (i.e., somatosensory cortex, SCx). Here, we adapted this paradigm to explore another cortical region known for playing an important role in perception of bodies, the motor cortex. To this aim, we recorded visual and motor-cortical potentials during the active maintenance of body and non-body-related images in WM. The motor-cortical responses were elicited by a task-irrelevant key pressing that was performed during the retention interval of body and non-body-related images in WM. These motor-cortical potentials (MCPs) resemble the readiness potential (Deecke et al., 1976), an intricate component arising from motor cortices and known to expose the underlying processing of one's forthcoming motor responses, the difficulty of an executed or imagined action (Kranczioch et al., 2009, 2010), as well as others' observed bodily actions (van Schie et al., 2004). Remarkably, MCPs allowed us to probe the state of the motor cortex in a visual WM task by dissociating the underlying process from other on-going EEG components (see methods section *Chapter 4*).

Background and aims of Chapter 5: Disrupting sensorimotor processing during WM for body and non-body-related images. In the previous chapters I examined cortical potentials of somatosensory and motor cortices, two of the brain regions that could potentially underpin a WM system for visually perceived body information. Nevertheless, while our EEG studies showed contralateral involvement during encoding and maintenance of hand images in WM, earlier studies from Smyth and colleagues indicated general involvement of the sensorimotor system. Specifically, the authors showed that either hemisphere (contralateral and ipsilateral) seems to be responsible for the maintenance of visually perceived body postures and actions in WM.

In this chapter we aimed to investigate whether or not contralateral sensorimotor areas, which showed enhancement of activity during encoding and maintenance in the two EEG studies of this thesis, support memory maintenance of the stimuli in WM. In other words, do the contralateral left/right sensorimotor hemispheres support encoding of subsequent

right/left hand images? To explore such somatotopic mechanisms, we created three different behavioural experiments that were based on the previous EEG studies. In each of these experiments, we interfered with the hypothetical sensorimotor processing of body images by adding a secondary task. The secondary task was performed during the maintenance of the stimuli in WM and executed by moving one hand (experiment 1 and 2) or both hands (experiment 3). The purpose of the secondary task was to interrupt sensorimotor processing through exhaustion of computational resources. If sensorimotor cortex supports memory maintenance of hand images in a somatotopic manner (i.e., following contralateral processing), memory performance for right hand images would be lower when moving the right hand than when moving the left hand (experiment 1 and 2, *Chapter 5)*. On the contrary, if sensorimotor cortex supports memory maintenance of hand images in a more general fashion (i.e., irrespective of laterality conveyed in the hands), memory performance for right hand images would be similar when moving the right hand and left hand.

6.3. Summary of results

In the following section I summarise the main results of the three studies presented in this thesis. The results of the first two EEG studies are divided according to the type of brain activity evoked in the experiment. The results of the behavioural study in Chapter 5 are described according to the experiment version (1 to 3). As a reminder, the analyses of all three studies were centred on analysing the effects of memory load and stimulus conditions (shape and hand images).

Chapter 3 - Neural dissociation for visual and sensorimotor WM: somatosensory brain areas

Visual-evoked potentials (VEPs) from visual-only trials. Approximately 300ms after the visual onset of the shapes and hands stimuli, the mean amplitude waveforms increased until the end of the retention interval over posterior electrodes. In the shape stimulus

conditions, this activity was higher when encoding 2 shapes than only 1. Conversely, no differences were observed when encoding hand images. Independently of the memory load (i.e., 1, 2), similar sustained activity was observed in the hand stimulus condition.

Somatosensory-evoked potentials SEPs (VEPs free) from visual-tactile trials. Analyses of variance in SEPs, after subtracting carry over visual effects from VEPs contained in the visual-tactile condition, yielded a significant Hemisphere X Load X Stimulus interaction. The follow-up analyses showed a significant interaction between memory load and hemisphere in the hand stimulus condition over posterior parietal electrode sites. Brain amplitudes increased from load 1 to 2 in the contralateral hemisphere. No differences were found in the shape condition. Further analyses confirmed the specificity of the SEPs modulation by memory load. We applied CSD and analysed pair of electrodes across more posterior and anterior electrode sites; no significant effects were found.

Despite the stimuli conditions being matched in memory performance, our results showed that only body stimuli elicited modulation of brain activity by memory load over SCx whereas non-body stimuli modulated activity over visual cortices.

Chapter 4 - Sensorimotor recruitment during WM for body and non-body-related images

Visual-evoked potentials (VEPs) from visual-only trials. The results showed an occipital-parietal peak in the time window 300-800ms (during the retention interval) in both stimuli conditions. The analyses of variance yielded significant differences between memory load 1 and 2 in both stimuli conditions. VEPs increased from load 1 to load 2 and no differences between stimuli conditions were found.

Motor-cortical potentials MCPs (VEPs free) from visual-motor trials. After subtracting carry over visual effects from VEPs contained in the visual-motor condition, the analysis of MCPs' variance yielded a significant Hemisphere X Load X Stimulus X ROI x Electrode

interaction. The follow-up analyses showed a significant difference between memory loads only in the hand stimulus condition over the contralateral frontal electrodes site. No differences were found in the shape condition, which activity did not differ from zero (i.e., no differential brain activity).

Last, similar to the first EEG study, there were not behavioural differences between stimuli conditions and only body stimuli elicited modulation of brain activity by memory load over body-related cortical regions, in this particular case, over motor cortices.

Chapter 5 - Disrupting sensorimotor processing during WM for body and non-body-related images.

Experiment 1. The results showed similar memory performance whether or not the participants moved the left or right hand while maintaining left or right hands in WM. Hence, recalling differences between left and right hand images while respectively moving left and right hands (i.e., congruent suppression) did not differ from doing the same in the absence of matching laterality between participants' moving hand and the hand images on display.

Experiment 2. Compared to the previous behavioural experiment, here the sample size and the difficulty of the hand movement were increased. Also, additional measures such as RT and memory performance for the control shaped stimuli were included. Similar to experiment 1, participants' performance did not differ whether or not their lateralized hand movement matched and the laterality of the left or right hand images to-be-remembered. The absence of a specific somatotopic motor suppression was also observed in the shape stimulus condition. The only significant difference was found as a main effect of stimulus condition, in which regardless of memory load and congruency of the dual task/suppression, performance was lower in the hand stimulus condition.

Experiment 3. Compared to the previous behavioural experiments, there was no factor of congruency. The motor suppression was performed simultaneously with both hands or not performed (i.e., absence or presence of bimanual suppression). Similar to the previous experiments, analyses of participants' memory performance did not yield significant results. Beyond the already expected effects of load, no main effects and interactions were found. Nevertheless, the analyses of RTs revealed a significant triple interaction (i.e., stimulus X memory load X movement). Here, only in the hand stimulus condition, participants were increasingly slower across memory loads (1 to 3) when exerting the bimanual motor suppression.

6.4. Interpretations and discussion

6.4.1. The role of somatosensory and motor cortex in processing visually driven body-related information

In two different EEG studies, we found significant interactions between mean amplitudes of sustained activity and memory load. Such interactions were found in the hand stimulus condition over somatosensory and motor cortices, respectively. This suggests that somatosensory and motor cortices may play a role in encoding and maintaining visual body-related information in WM. Conversely, these body-related cortical regions did not exhibit effects of memory load in the shape stimulus condition. These findings are consistent with current accounts in WM, proposing that perceptual mechanisms shaped by experience are key to encode and maintain stimuli in WM (D'Esposito and Postle, 2015). Here I speculate that SCx and motor cortices represent at least some of the dimensions that correspond to the whole percept conveyed in body-related stimuli. This is probably underpinned and modulated by exposition and functional associations between one's experience and others' bodies. Such recurrent perceptual stimulation is probably stored as sensory associations between tactile and motor sensations and the view of bodies

Our results do not imply that other brain areas (e.g., extrastriate body area, EBA; Downing et al., 2001) could participate in representing a bodily percept over time, but suggest that functionally-relevant perceptual cortices other than visual may well contribute to memory maintenance of visual information. Importantly, by functionally-relevant I mean that these brain regions (i.e., sensorimotor) are known to be shaped and participate in perceptual long-lasting associations, as well as in functional interactions in several cognitive domains that involve use of our own body beyond purely WM tasks.

6.4.2. Subtraction of evoked potentials: visual, somatosensory, and motor-cortical potentials

The aforementioned EEG results were obtained after subtracting VEPs from visual-only trials to a conjunction of VEPsSEPs (visual-tactile trials; in Chapter 3) and VEPsMCPs (visual-motor trials; in Chapter 4). These subtractions allowed us to dissociate SEPs and MCPs from those VEPs generated at the sight of the visual stimuli, as well as, to perform analyses of mean amplitude waveforms arising from somatosensory and motor regions during visual processing of body and non-body-related stimuli. Here, it is important to emphasize that subtractions add a certain amount of noise to the data; noisy meaning that such data cannot be understood and interpreted accurately. In the current studies, there are several possible sources of noise:

(1) In the first EEG study – Chapter 3, we subtracted VEPs elicited in the visual-only trials from VEPsSEPs (visual and concurrent somatosensory-evoked potentials) elicited in the visual-tactile trials. We assumed that such subtraction reflects pure SEPs, which are modulated by the visual content of the task. Nevertheless, distinctive cognitive processes could underlie visual-only trials and visual-tactile trials. In such case VEPsSEPs minus VEPs would not reflect pure SEPs, but an additional and unknown measure. Specifically, we could have 'manufactured' a cognitive subtraction, which often neglect interactions between cognitive processes, tasks, and neural systems (Friston el al., 1996; Friston et

al., 1997). We minimised these effects by reducing task differences (i.e., the tactile stimulation was task-irrelevant). We explained and emphasized to the participants that the tactile taps were irrelevant. Moreover, white noise was played during the whole task to mask possible confounding on the recording such as attentional shifts or auditory evoked-potentials. Importantly, the behavioural results showed that participants perform equally across visual-only and visual-tactile trials.

(2) In the second EEG study – Chapter 4, we subtracted VEPs elicited in the visual-only trials from VEPsMCPs (visual and concurrent motor-cortical potentials) elicited in the visual-motor trials by the participants' key pressing during the retention interval of the task. In this study, there was a difference in behavioural performance. As expected, participants' performance in the visual-motor trials was lower than in the visual-only trials. The task-irrelevant key pressing used to elicit a motor-cortical potential corresponded to a dual task with higher complexity compared to the single task (i.e., memory task). Therefore, distinctive cognitive processes do underlie the subtraction between brain activity from visual-only trials and visual-tactile trials. VEPsMCPs minus VEPs would not reflect pure MCPs, but additional factors than contain among others, difficulty and effort. Nevertheless, we considered these effects by matching the difficulty of the stimuli types. Therefore, the dissimilarities found in brain waveforms between holding in WM shape and hand images are likely due to the type of information delivered in the percept (i.e., body or non-body related).

6.4.3. Visual contralateral delay activity (vCDA) in the present experiments

In both EEG studies we found increasing activity, starting 300ms after the onset of the stimuli, which persist in form of a sustained waveform for the whole retention interval. This activity, specifically, visual contralateral activity (vCDA) was recorded from posterior visual electrode sites similar to those used in previous studies (Todd and Marois, 2004;

McCollough et al., 2007; Tsubomi et al., 2013). Despite the present two EEG experiments having used the same stimuli and the main memory task was similar, the results of the vCDA led to different results. In the first study, the vCDA was not modulated by memory load in the hand stimulus conditions whereas in the second study, the index of WM maintenance was significantly modulated by load. The reasons for such difference (between experiments) are not clear. Yet, here I postulate a number of possible causes:

i) *Memory systems and subsequent encoding are malleable:* In the second EEG experiment, we found modulation of VEPs and vCDA in the visual-only trials for the hand stimulus condition. In this experiment, the motor system was already needed to produce the task-irrelevant key pressing that elicited the MCPs in the visual-motor trials. Even if the key pressing was specifically executed in the latter trials, these could have primed the encoding scheme in the visual-only trials. Then, the motor cortex could have been 'virtually suppressed' even in the absence of a task requiring its use. In this sense, the MCPs reported in Chapter 4 could reflect a form of interference rather than encoding *per se*, which is still indicating that motor regions were engaged.

ii) *Small changes in perceptual settings:* the distance of the stimuli from the center of the visual display was smaller in the second experiment. The visual stimuli were displayed one degree less towards the right and left hemifield. (5° compared to 6° in the first experiment). Since hand images were less peripheral, encoding could have switched to a more advantageous visual strategy. Another difference between experiments 1 and 2 is the position of the participants' hand. In the second experiment, the hands were palm down whereas in the first one these were matching the posture of the hands in the display by being palm up. These modifications may well explain the differences in the visual engagement, as portrayed by the differential vCDA, across the EEG experiments.

In consistency to the plasticity of perceptual and memory systems, as well as the effect of small modifications across paradigms, percepts are likely to be encoded depending on

previous sensory associations, top-down processes, as well as specific task-demands. For instance, Gao et al. (2014) showed engagement of motor cortices during WM for biological motion (i.e. actions in form of points of light display) and how later verbal encoding of these stimuli prevented motor cortices from participating in WM encoding. In another study, Tessari and Rumiati (2004) showed that encoding of meaningless and meaningful actions relies on distinct mnemonic routes. They prompted participants to use one or the other route by manipulating the order of presentation and proportion of the stimuli to be remembered, showing that when trials of meaningless and meaningful actions were mixed, memory performance reflected the expected performance for that system that would allow it to accomplishing both tasks. More recent studies further emphasize the close relationship between visual systems and more frontal regions. Wurm and Lingnau (2015) showed that visual regions such as inferior parietal and occipito-temporal cortex can be decoded for abstract levels of actions while premotor cortex is for concrete levels of actions (i.e., specific kinematics). Overall, WM seems supported by a distributed and flexible network of brain regions (Christophel et al., 2017).

6.4.4. Contralateral processing of visually perceived and lateralised body stimuli

The previous EEG experiments showed an effect of memory load in the hand stimulus conditions over the contralateral somatosensory and motor cortices. This is indicated by the significant interaction of Hemisphere X Memory load. Such results suggest that right hands, displayed on the right hemifield were encoded in the left hemisphere, and left hands shown on the left hemifield were in the right hemisphere. In the last behavioural study, we investigated this by conducting three behavioural versions of the previous EEG studies. The results of these three experiments suggest an overall processing of the hand images (i.e., an absence of contralateral processing). This goes in coherence with Smyth and Pendleton (1988), but does not support our previous experiments and other evidence

for a more somatotopic and contralateral processing of visually perceived hands (Kalénine et al., 2010; Ortigue et al., 2010).

It is somewhat possible that the contralateral effects observed in our EEG data were partially driven by the manipulation of the data. We averaged data from contralateral and ipsilateral activity under the assumption that contralateral activity from trials cuing to the right containing right hands and trials cuing to the left containing left hands possessed similar brain activity (and *vice versa* for ipsilateral activity). To explore this issue, contralateral and ipsilateral activity needs to be teased apart. This implies the design of further experiments with enough trials for each of the aforementioned experimental conditions.

6.5. Overall limitations and further developments

While the present PhD work sheds some light on several research questions, it also open new challenges, possibilities, and questions that require further exploration. In the discussion of each individual chapter I detailed some of the potential and specific limitations of the corresponding study (namely, the problematic interpretation of sustained activity, the lack of information in our data about specific mnemonic content, the measurement of RT and trade-off effects in the behavioural study, and the inherent problems of data interpretation in subtractive methods/paradigms). In the following section I comment on more general aspects. Here I revisit limitations that concern the overall work of this thesis, as well as offering new ways to overcome these.

6.5.1. Alternative measures of WM processing

The studies included in this thesis include measures of WM that are related to the participants' ability to discern signal from noise data (i.e., signal detection theory; *d'*). We used these measurements to make sure that stimuli and loads were matched across conditions (body *vs.* non-body-related). Other studies in the WM field have used different

parameters, indexes, and formulae, as well as greater memory load. For instance, the studies that inspired the work presented in this thesis used up to 10 visual stimuli and measured *K'* to measure WM capacity (Vogel et al., 2004). By including additional memory load it is possible to conduct further analysis linking participants' behavioural performance and their corresponding brain activity. Precisely, the CDA has been usually studied as neural marker of WM, reflecting a correlation between participants' memory capacity and the concomitant increasing brain amplitude. The current work did not intend to explore WM capacity for bodies and actions and the EEG and behavioural studies did not include experimental conditions with greater loads than 2 and 3. Therefore, in the context of the present experimental work, it is certainly difficult to fully understand the modulation of brain activity by memory load over body-related cortices.

6.5.1.1. *Estimates of K' – memory capacity*

Further work needs to include greater memory loads, the calculation of memory capacity (*K'*), and analyses of the correlation between behavioural and electrophysiological data; in this regards, several theoretical and practical aspects need to be considered. To start with, memory capacity has been classically framed in discrete-slots memory models, which conceptualise WM as a limited number of slots (i.e., available workspace) (Cowan, 2001). Researchers theorise on the variable number of slots that are used to retain stimuli to-be-remembered in WM and significant progress has been made by examining how different manipulations reduce the availability of workspace in WM, that is the memory capacity of the system. WM capacity have been usually measured by using the approach of Pashler (1988), as well as the derivate method of Cowan (2001). In brief, these approaches postulate that if observers can maintain in memory *K* items from an array of *S* items, then the changing item should be one of the items being maintained in memory on *K/S trials,* which should lead to a correct performance on *K/S of the changing (i.e., different) trials.* This approach takes into account the effects of guessing by considering hit

rate *H = hits/(hits + misses)* and the false-alarm rate *F = false alarms/(false alarms + correct rejections).* The expressed formulae is *K = S X (H - F)*, where *K is the WM capacity, S* is memory load (i.e., the size of the array), *H* is the hit rate, and *F* is the false alarm rate. By using this approach, a memory capacity of two to three items (i.e., approx. *K = 2.4)* has been reported in behavioural studies examining WM for body-related information (Wood, 2007; Wood 2008; Wood, 2011; Smyth 1990; Smyth 1988, Gao, Bentin and Shen, 2014).

In regards to the correct method to quantify memory capacity *K'*, it is necessary to consider the existence of two widely used types of delayed-to-sample match paradigms: single-probed recognition and whole-display recognition. These two versions do not only differ in the type of presentation but also in the type of information provided to the participant. Contrary to the whole-display recognition task, in the single-probed version the participants know which item may change and, consequently, the cognitive demands and the result of these two versions may differ. Precisely, Rouder et al. (2011) highlighted that effects of guessing in single-probed and whole-display recognition tasks need to be specifically corrected by following the approach of Pashler (1988) and the method of Cowan (2001), respectively. Contrasting their popular use, these methods are not rivals or substitutes; the type of experimental paradigm defines the choice. Secondly, relevant for the studies included in this thesis, the two methods of estimating memory capacity fail to assess small set sizes. In principle all participants have the capacity to retain one item in WM, however, computing the outlined methods results in $K < 1$ because these do not consider factors such as distractions and variability across conditions.

In summary, the studies of the current work include a small set size and subsequent memory load. This affects the scope of our studies by limiting the quantity of information that can be extracted form the data. Further studies need to consider tasks with greater memory loads and the further examination of the workspace required for such tasks (i.e.,

memory load). To this aim, the specific type of delayed-to-sample match paradigm needs to be taken into account.

6.5.2. Alternative measures combining WM and body-related processing

The EEG studies presented here provided us with evidence of differential brain activity, which was located across distinctive brain regions and concomitant to the number and type of stimuli to-be-remembered (body and non-body-related). In addition, the behavioural study provided us with further insight about the causal role of the brain areas examined in the electrophysiological studies. Nevertheless, there are two important limitations concatenating the three studies: i) the electrophysiological waveforms that we obtained (i.e., vCDA, vdCDA, vdN2cc, and MCPs) do not disclose whether or not such neural signatures are necessary to encode and maintain the stimuli in WM. Furthermore, ii) the behavioural studies that we designed to ascertain the previous point were unspecific. The motor suppression used here to interrupt the memory consolidation was performed continuously throughout the whole trial and without an exhaustive control of the speed and kinematics of the movement. Therefore, it is unclear when and how such motor suppression may have had an effect. It is here where additional techniques such as TMS and EMG recordings could support further research by disrupting/stimulating and recording the underlying sensorimotor process with exact and high temporal resolution

6.5.2.1. TMS to observe causal evidence of neural processing

Electromagnetic pulses (TMS) can be used to induce brief changes in the on-going processing of information. Then, if a brain area is responsible for a cognitive process, applying TMS at specific frequencies (e.g., 10Hz) can briefly disrupt the course of this process and a causal change in the outcome behaviour can be observed (e.g., lower memory performance/recall). Hence, it is possible to understand the role of different neural regions, shedding light on whether these are responsible for a cognitive process or

are just a mere correlation of other parallel activity. In the past, this approach has showed causal evidence for engagement of a distributed network of brain regions, including sensorimotor and more anterior motor cortices, during visual perception of human bodies (Urgesi et al. 2007; Avenanti et al. 2013). Conversely, applying TMS over visual areas only disrupted processing of bodies that were in non-canonical positions (i.e., inverted). This suggests that processing of bodies implies the embodiment of observed postures onto the observers' sensorimotor representations. In the context of the present experiments, TMS would disrupt and modulate memory performance for body stimuli when stimulation occurs over SCx during late time windows (i.e., 145, 300, 600ms), while no disruption of memory performance (or less disruption) should occur when participants are asked to remember polygonal shapes.

6.5.2.2. TMS uncovering motor processing - motor evoked-potentials (MEPs):

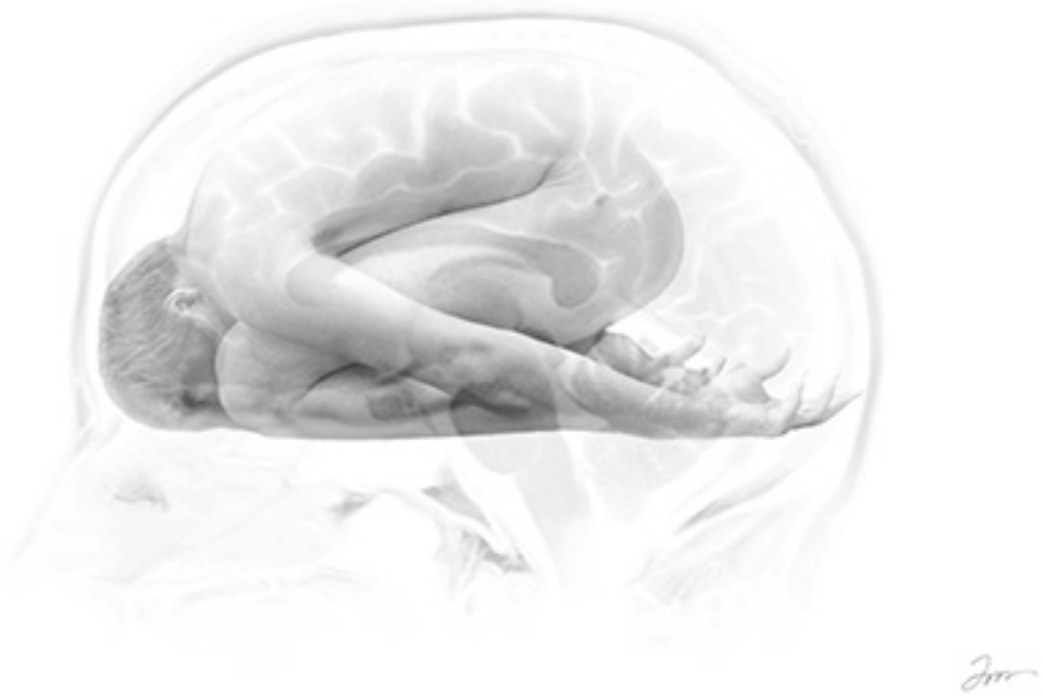
TMS can be also applied over the central scalp sites, reaching more focally motor cortices. This brain stimulation elicits the spinal cord and peripheral muscles to produce a neuro-electrical signal known as motor-evoked potential (MEP), which can be recorded by placing electrodes on different muscles of the participants' hand. In the past the strength and modulation of MEPs have been shown to reflect underlying motor processing when observing others' bodies and actions (Fadiga et al. 1995; Van Schie et al. 2004). In the context of this experiment, this can be further used to probe mnemonic storage of body-related information when participants hold in memory distinct number of visually depicted hand images.

6.6. Summary and conclusion

In summary, this thesis examined memory encoding of visual images conveying body-related information. We compared the processing of these images with that for non-body-related visual stimuli. Furthermore, we developed two novel paradigms that allowed us to

explore and dissociate the neural candidates for such mnemonic process. Specifically, we examined brain activity arising from visual and body-related cortical regions. By measuring VEPs, SEPs, and MCPs (i.e., visual, somatosensory, and motor-cortical potentials) in a WM task for body and non-body-related stimuli, we found distinct neural responses across the subsequent brain areas. The results showed that beyond visual brain areas, sensorimotor regions over posterior and more frontal cortices were modulated by memory load when holding in memory body-related stimuli (i.e., hand images). Then, we developed a behavioural study to further examine the aforementioned EEG results. We found evidence of a trade-off effect between a task-irrelevant motor suppression and the encoding of body-related images, which convey motor information. Nevertheless, the specific somatotopic organisation of the encoding and maintenance of the stimuli in WM needs further inspection. Altogether, we provide original evidence for a WM processing based on sensorimotor associations as a precursor of persistent neural activity. While previous studies have shown that visual information elicits modulation by memory load in posterior and visual cortices (Todd and Marois, 2004; Vogel and Machizawa, 2004; McCollough et al., 2007; Tsubomi et al., 2013) and tactile information in somatosensory cortices (Harris et al., 2002; Katus et al., 2015; Katus and Eimer, 2016) our results suggest a more dynamic process, in which the memoranda elicits prior sensory associations, involving neural recruitment over and above perceptual-input cortices.

6.7 Artistic Impressions VI



Bodily Realm - The Reason Why (2015). Photography on board (42 x 29cm) / AGP

The human brain exists for two reasons: to generate complex body movements, and to process others' movements. Both processes underpinned slightly similar neural mechanisms, which are fundamental to experience our dynamic social environment.

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Enjoy life!

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